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Hepatic 7-ethoxyresorufin-*O*-deethylase activity, plasma steroid hormone concentrations, and liver bioassay-derived 2,3,7,8-TCDD toxic equivalent concentrations in wild white sucker (*Catostomus commersoni*) caged in bleached kraft pulp mill effluent

M.R. van den Heuvel, K.R. Munkittrick, G.J. Van Der Kraak, M.R. Servos, and D.G. Dixon

Abstract: Prespawning male white sucker (*Catostomus commersoni*), captured near Jackfish Bay, Lake Superior (exposed to bleached kraft pulp mill effluent (BKME)), and Mountain Bay (reference) were caged in the BKME receiving area for 2, 4, and 8 d. Initially, the hepatic 7-ethoxyresorufin-*O*-deethylase activity was similar in fish from both BKME and reference sites and, upon BKME exposure, increased 20-fold at both sites after 2 d. The H4IIE cell culture bioassay was used to measure 2,3,7,8-tetrachlorodibenzo-*p*-dioxin toxic equivalent concentration (TEC) in sucker liver extracts. H4IIE bioassay-derived TECs from Jackfish Bay sucker showed no significant treatment differences; combined TECs for all treatments averaged 51.1 pg·g^{-1}. Mountain Bay sucker liver TECs were initially significantly less (4.64 pg·g^{-1}) than the Jackfish Bay TECs but did show a significant, fivefold increase when fish were exposed to effluent. Mountain Bay and Jackfish Bay 8-d BKME-exposed fish showed no uptake of TECs calculated from directly measured polychlorinated dibenzo-*p*-dioxins (PCDDs) and dibenzofurans (PCDFs) during this exposure. The results suggest that PCDDs and PCDFs are not responsible for the mixed function oxidase induction observed. Handling stress caused rapid reduction of the plasma steroids testosterone and 11-ketotestosterone, confounding any possible BKME effect.

Résumé : Des meuniers noirs (*Catostomus commersoni*) capturés avant la fraye près de la baie Jackfish, dans le lac Supérieur (exposés às des effluents d'usines de pâte kraft blanchie (EUPKB)) et dans la baie Mountain (témoins) ont eté mis en cage dans la zone recevant des EUPKB pendant 2, 4 et 8 jours. Au début, l'activité de la 7-éthoxyrésorufine-*O*-déséthylase hépatique, qui était semblable chez les poissons provenant de la zone EUPKB et chez les témoins, a augmenté d'un facteur de 20 chez les deux groupes après 2 jours d'exposition aux EUPKB. On s'est servi d'un essai biologique (culture de cellules H4IIE) pour mesurer la concentration de toxiques équivalente (CTE) à celle de la 2,3,7,8-tétrachlorodibenzo-*p*-dioxine dans des extraits de foie des meuniers. Les CTE obtenues dans le cadre des essais biologiques sur H4IIE ont montré que le traitement n'était pas responsable de différences significatives chez les meuniers provenant de la baie Jackfish; les CTE combinées (tous les traitements) atteignaient en moyenne 51,1 pg·g^{-1}. Les CTE mesurées dans le foie des meuniers de la baie Mountain étaient au départ significativement

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inférieures (4,64 $pg \cdot g^{-1}$) à celles mesurées chez les meuniers de la baie Jackfish, mais elles ont augmenté significativement d'un facteur de cinq après que les poissons ont été exposés aux effluents. Les poissons de la baie Mountain et de la baie Jackfish exposés pendant 8 jours à des EUPKB n'ont pas montré une absorption plus élevée de leurs CTE calculées à partir d'une mesure directe des polychlorodibenzo-*p*-dioxines (PCDD) et des polychlorodibenzofuranes (PCDF) au cours de cette exposition. Ces résultats indiquent que les PCDD et les PCDF ne sont pas responsables de l'induction des oxydases à fonction mixte observée. Le stress lié à la manipulation des poissons a causé une diminution rapide de leurs concentrations plasmatiques de testostérone et de 11-cétotestostérone, masquant ainsi tout effet éventuel des EUPKB.

[Traduit par la Rédaction]

Introduction

The most consistently measured effect of bleached kraft pulp mill effluent (BKME) on fish populations has been elevated levels of a mixed function oxygenase (MFO) enzyme, P4501A (Rogers et al. 1989; Lindström-Seppä and Oikari 1990; Smith et al. 1991; Hodson et al. 1992; Munkittrick et al. 1994). Various studies have also shown effects on reproduction of fish exposed to BKME ranging from population (Andersson et al. 1988; Karås et al. 1991; McMaster et al. 1991; Munkittrick et al. 1991; Adams et al. 1992) to biochemical levels (McMaster et al. 1991; Munkittrick et al. 1991; VanDer Kraak et al. 1992).

Fish populations in Jackfish Bay, Lake Superior, have demonstrated biochemical and reproductive changes in association with exposure to a BKME receiving area (McMaster et al. 1991; Munkittrick et al. 1991, 1992*a*, 1992*b*, 1994). Elevated levels of P4501A have been measured in wild white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*) and lake whitefish (*Coregonus clupeaformis*). P4501A induction has remained consistent despite the installation of secondary treatment (1989) and increased levels of chlorine dioxide substitution (1990) (K.R. Munkittrick, unpublished data). Reproductive effects observed in BKME-exposed white sucker at Jackfish Bay include increased age to sexual maturity, reduced secondary sex characteristics, smaller gonads, lower fecundity with age, and reduced levels of plasma steroid hormones (McMaster et al. 1991; Munkittrick et al. 1991, 1994) relative to fish from two Lake Superior reference sites. Detailed mechanistic evaluation has also shown reduced in vitro steroid hormone synthesis and reduced plasma gonadotropins in association with exposure to BKME (Van Der Kraak et al. 1992).

The induction of the P4501A enzyme is mediated through a cellular receptor, the Ah receptor. Mammalian studies have indicated that the majority of toxicological effects of many planar halogenated hydrocarbons (PHHs) are mediated through the binding of PHHs to the Ah receptor (Goldstien and Safe 1989; Hahn and Stegeman 1992). Ah receptor binding results in the subsequent expression of a battery of genes (Nebert et al. 1990). The CYP1A1 gene is perhaps the best known of the Ah gene battery and its resultant MFO enzyme (P4501A) is ubiquitous in toxicological literature. The relationship of MFO induction to other more serious effects remains controversial. No direct links have been found between increased MFO activity and altered reproductive performance. It is generally held that MFO induction is a sensitive biochemical indicator of exposure to PHHs and polyaromatic hydrocarbons (PAHs). Through the Ah receptor, MFO induction may share a common mechanism with other more severe effects, including reproductive dysfunction. Although MFO induction on its own may not be detrimental to an organism under most circumstances, we view it as an indication that other, possibly more severe, biochemical alterations are occurring.

The chemical composition of BKME is complex and little progress has been made in determining causative agent(s) of elevated P4501A or reproductive alterations in fish. Correlations have suggested that polychlorinated dibenzo-*p*-dioxins (PCDDs) and dibenzofurans (PCDFs) are prime candidates for causing elevated levels of P4501A and reproductive impacts in fish exposed to BKME (Rogers et al. 1989; Servizi et al. 1993; Servos et al. 1994; van den Heuvel et al. 1994). PCDDs and PCDFs are potent inducers of P4501A enzymes in fish (van der Weiden et al. 1992; Parrott et al. 1993) and cause reproductive dysfunction in mammals (Bookstaff et al. 1990; Moore et al. 1991; Mably et al. 1992). Such correlative evidence has lead to a general acceptance that PCDDs and PCDFs are a prime cause of the sublethal effects observed in fish.

Recent empirical data suggest that PCDDs and PCDFs may not be exclusively involved in P4501A induction. P4501A induction occurs rapidly (<2 d) and disappears rapidly in fish exposed to BKME (Munkittrick et al. 1995). P4501A mRNA has also been observed to increase rapidly (<2 d) in Atlantic tomcod (*Microgadus tomcod*) exposed to pulp mill effluent (Courtenay et al. 1993). When fish were placed in clean water, levels of P4501A mRNA cleared more rapidly in pulp mill exposed tomcod than in fish injected with 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (2,3,7,8-TCDD). Temporary mill shutdown has also caused reduction of elevated P4501A enzymes and recovery of plasma steroid hormone levels (Munkittrick et al. 1992*b*). Elevated levels of P4501A and reduced steroid hormones have also been observed at mills that do not use chlorine in the bleaching process (Munkittrick et al. 1994). In the same study, fish with background levels of PCDDs and PCDFs showed significant 7-ethoxyresorufin-*O*-deethylase (EROD) induction (Munkittrick et al. 1994; Servos et al. 1994). PCDDs and PCDFs are known to be highly lipophilic and poorly metabolized; uptake and depuration are very slow (Muir et al. 1990; Opperhuizen and Sijm 1990). Thus, the slow kinetics of these compounds would seem to preclude their involvement in the rapid biochemical changes noted here. These results, although not conclusive, cast doubt

on the sole involvement of PCDDs and PCDFs in biochemical effects observed in fish exposed to BKME.

Further study of the cause–effect relationships of compounds in BKME with observed biological effects requires a measure of exposure that is related to the observed biological response, and considers chemicals that are not routinely measured by analytical chemistry. The H4IIE rat hepatoma bioassay (Tillitt et al. 1990, 1991; van den Heuvel et al. 1994) measures the in vitro P4501A-inducing ability of extracts from environmental samples relative to the potency of 2,3,7,8-TCDD. The measurement of 2,3,7,8-TCDD toxic equivalent concentrations (TECs) by this means has the advantage of integrating the biological potency of the mixture of chemicals in the sample, including structurally similar P4501A-inducing compounds.

The objective of this study was to examine short-term temporal changes in the P4501A MFO enzyme activity of fish exposed to BKME while simultaneously using the H4IIE bioassay as a broad method of measuring exposure to P4501A-inducing compounds. This was achieved by caging wild prespawning male white sucker in the receiving area of a bleached kraft mill. Direct analytical measurements were used to determine if PCDDs and PCDFs were accumulated in parallel with bioassay-derived TECs. This work also examined the impact of receiving water exposure on levels of plasma reproductive steroid hormones.

Materials and methods

Fish caging and sampling

Prespawning male white sucker were captured in Sawmill Creek, the spawning stream adjacent to Jackfish Bay during May 1993. This bay is the receiving area of bleached kraft pulp mill effluent from the mill in Terrace Bay, Ont., and Sawmill Creek is the only suitable spawning location adjacent to the bay (McMaster et al. 1991, 1992; Munkittrick et al. 1991). Sawmill Creek is not exposed to effluent (Fig. 1). White sucker were also captured from a reference location, the Little Gravel River, which flows into Mountain Bay, a small bay on Nipigon Bay, Lake Superior. Sucker were caught overnight in hoopnets as they entered the spawning stream.

White sucker were transported by truck from the capture site at Mountain Bay to Sawmill Creek in an aerated plastic tank (2-m^3 capacity). Fish from both Jackfish Bay and Mountain Bay were held in circular wire mesh cages (1-m^3 capacity) in Sawmill Creek until experimental caging began (<1 d). Thirty sucker from both Sawmill Creek and Mountain Bay were transported by boat to the mouth of Blackbird Creek, where effluent enters Jackfish Bay. Fish were suspended in the water column in wire mesh cages approximately 25 m from the mouth of Blackbird Creek. Ten fish from each site were sampled at 2, 4, and 8 d after caging began. Controls (0 d) were sampled within 12 h of capture in their respective spawning streams. To control for effects of caging, a group of ten sucker from each site were kept caged in Sawmill Creek and were sampled at 4 d; sampling of these fish at 2 and 8 d was not conducted.

Sixteen sucker from each site were dosed with β-naphthoflavone (β-NF) as positive controls for MFO induction. Four fish from each of the two groups were injected intraperitoneally with 0.5, 5, and 50 $mg \cdot kg^{-1}$ β-NF and also with triolein carrier alone. Fish were held in Sawmill Creek until sacrifice at 4 d.

A final group of 16 sucker from each site was transported to the University of Waterloo (approximately 1500 km). Fish were separated according to site of capture into two flowthrough (10 $L \cdot min^{-1}$), aerated fibreglass tanks (3-m^3 capacity) receiving University of Waterloo well water. Fish were sampled 21 d after the date of capture. Nine fish from Mountain Bay died prior to sampling, there were no mortalities in the fish from Jackfish Bay.

White sucker were rendered unconscious by a blow to the head prior to necropsy. Blood for steroid analysis was obtained by caudal artery puncture using a 5 mL syringe with a 22 gauge needle. Blood was stored in a heparinized vacutainer on ice prior to centrifugation in a clinical centrifuge. Plasma was frozen in liquid nitrogen. Fish weight, fork length, gonad weight, and liver weight were recorded, and an operculum was removed for aging. White sucker livers were excised and divided into two subsamples. One gram of liver for MFO analysis was placed in a 2 mL cryovial and immediately frozen in liquid nitrogen. The remaining liver was wrapped in aluminum foil (previously fired at 400°C) and stored at −20°C pending analysis.

Enzyme and steroid analysis

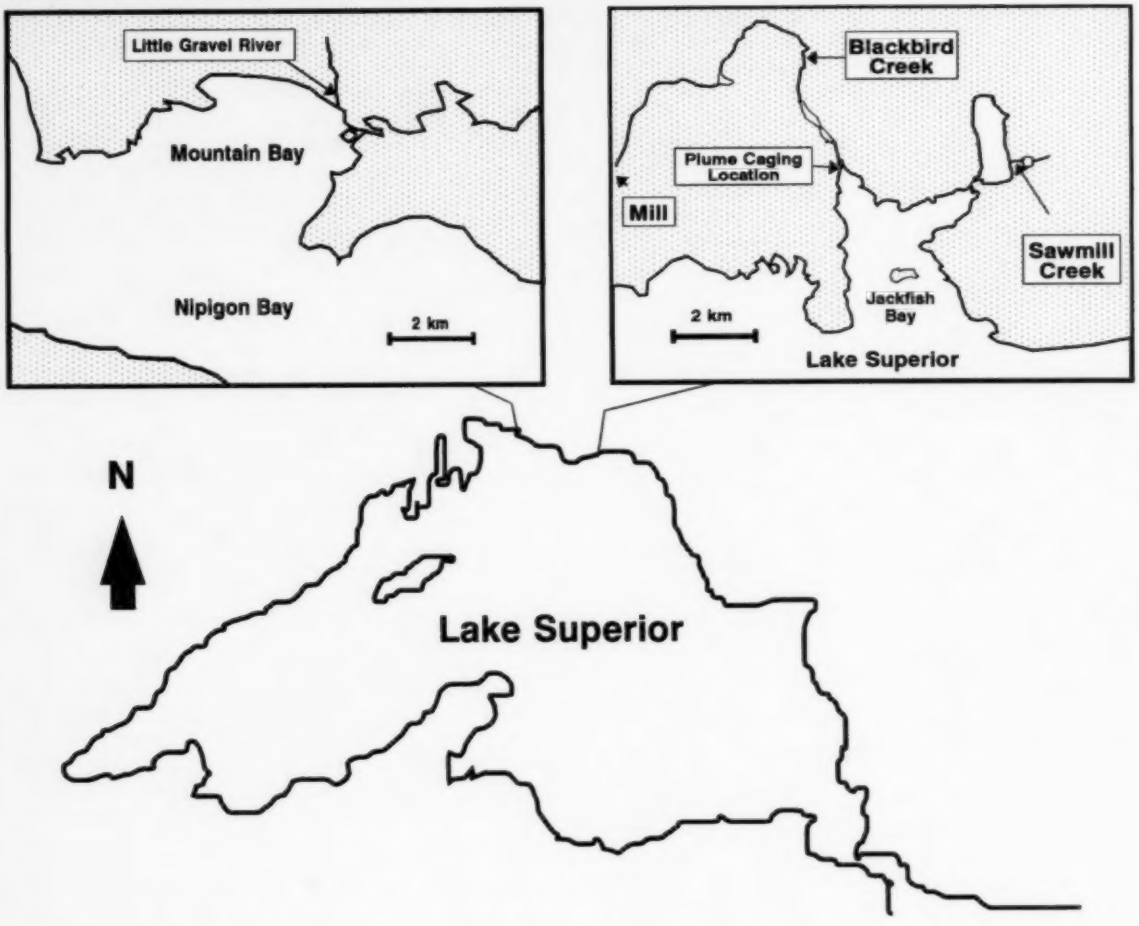
Hepatic MFO activity was quantified as EROD using a modification of the method of Pohl and Fouts (1980). Reagent concentrations in the reaction mixture were: 7-ethoxyresorufin, 1.7 μM (Sigma, St. Louis, MO); NADPH, 0.5 mM (Boehringer Mannhiem, Germany); $MgSO_4$, 17 mM; and HEPES, 0.1 M, pH 7.8. EROD analysis was performed on the postmitochondrial supernatant of white sucker liver in 48 well plates using a Millipore Cytofluor 2350 plate reader fluorometer with excitation filter 530 nm and emission filter 590 nm. The reaction was terminated using methanol. Activity was determined at 25°C using approximately 0.2 mg of protein (postmitochondrial supernatant). Activity was normalized for protein, which was measured using the Bradford (1976) protein assay.

The blood plasma concentrations of testosterone and 11-ketotestosterone were determined according to RIA protocols previously described (Van Der Kraak et al. 1984, 1990; Wade and Van Der Kraak, 1991).

Tissue extraction and sample preparation for the H4IIE bioassay

Liver samples were weighed and ground with sodium sulphate (previously fired at 400°C). Samples were soxhlet-extracted with methylene chloride in a prerinsed apparatus. Sample cleanup was performed according to van den Heuvel et al. (1994). This method used gel permeation chromatography (GPC, Biorad SX-3 GPC resin, Richmond Calif.) to remove lipids followed by chromatography on basic alumina adsorbent (Fisher, Fair Lawn N.J., activity I). The lipid content was estimated by evaporating the first GPC fraction to a constant weight. The final extract was

Fig. 1. Jackfish Bay and Mountain Bay study sites.



concentrated into 50 μL of dimethylsulfoxide (DMSO). Serial dilutions with DMSO were made from the final extract to yield a total of seven doses. A procedural blank was run with every set of extractions; any procedural blank contamination that occurred was found to be insignificant and no correction was applied.

The recovery of several classes of MFO-inducing compounds using the GPC–alumina cleanup is given in Table 1. Recovery experiments were performed in order to demonstrate that PCDDs, PCDFs, polychlorinated biphenyls (PCBs), and PAHs (the three most common classes of MFO-inducing compounds) all show good recovery using the cleanup method described. Recovery for 2,3,7,8-TCDD was determined using tritiated TCDD. The recovery of seven non- and mono-ortho PCBs was determined using a Varian 3400 GC equipped with an electron capture detector. PCBs were eluted on a Supelco DB-5 capillary column (30 m, 0.25 mm ID). PAH compounds were measured on a Shimadzu HPLC equipped with a photodiode array using a C-18 column.

H4IIE bioassay procedure

Rat hepatoma (H4IIE) cells (American Type Culture Collection, CRL 1548) were cultured using the media described by Tillitt et al. (1990). Bioassays were performed in Costar 48-well plates. Cells were plated at a density of 50 000 cells per well in 0.5 mL of media. Four 2,3,7,8-TCDD (Cambridge Isotope Laboratories, Woburn, Mass.) dose–effect curves were run concurrently with every bioassay. The concentration of the 2,3,7,8-TCDD stock solution was confirmed using GC-MS. All values given in this paper are based on measured concentrations of the 2,3,7,8-TCDD standard. Each standard curve exposed cells to 0.244, 0.488, 0.967, 1.95, 3.91, 7.81, and 15.6 pg·well^{-1} of 2,3,7,8-TCDD. Sample bioassays used seven dilutions of the liver extracts tested (1.56, 3.13, 6.25, 12.5, 25.0 ,50.0, and 100%). Wells were dosed in triplicate 24 h after plating in 2.5 μL of DMSO containing the extracts or 2,3,7,8-TCDD standards. After 48 h, the cells were analyzed for EROD activity. Media was aspirated from the wells and cells were rinsed with phosphate buffered saline. EROD

Table 1. Mean recoveries for 2,3,7,8-TCDD, a select group of non- and mono-ortho polychlorinated biphenyls (PCB) and polyaromatic hydrocarbons (PAHs) using a GPC/alumina sample cleanup.

Compound	Mean recovery (%)[a]	Method of analysis
2,3,7,8-tetrachlorodibenzo-*p*-dioxin	96.0	[^{3}H]-TCDD
3,4,4′,5-trichlorobiphenyl (PCB 81)	99.0	GC-ECD
3,3′,4,4′-tetrachlorobiphenyl (PCB 77)	100.8	GC-ECD
2,3,3′,4,4′-pentachlorobiphenyl (PCB 105)	94.4	GC-ECD
2,3′,4,4′,5-pentachlorobiphenyl (PCB 118)	102.0	GC-ECD
3,3′,4,4′,5-pentachlorobiphenyl (PCB 126)	98.2	GC-ECD
2,3,3′,4,4′,5-hexachlorobiphenyl (PCB 156)	99.9	GC-ECD
3,3′,4,4′,5,5′-hexachlorobiphenyl (PCB 169)	101.8	GC-ECD
Naphthalene	56.1	HPLC/diode array
Chrysene	96.0	HPLC/diode array
Benzo[*a*]pyrene	94.4	HPLC/diode array
Dibenzo[*a*,*i*]pyrene	2.9	HPLC/diode array
3-methylcholanthrene	91.7	HPLC/diode array
β-Naphthoflavone	37.9	HPLC/diode array

[a]Sample sizes: $n = 8$ for 2,3,7,8-tetrachlorodibenzo-*p*-dioxin; $n = 6$ for the remaining compounds.

activity was determined in the 48-well plates with the cells still attached at 37°C. The reaction mixture was identical to that previously described in this study for fish liver EROD analysis. A kinetic assay with an incubation time of 10 min was performed using a Millipore Cytofluor 2350 plate reading fluorometer as previously described. Protein was determined by a modified fluorescamine method against a BSA standard (Lorenzen and Kennedy 1993). The EROD reaction mixture was aspirated off and 250 μL of distilled water added to the cells. After allowing the cells to swell for at least 5 min, plates were frozen at −75°C to detach and lyse cells. Cells were thawed and 0.5 mL of 0.5 M potassium phosphate buffer, pH 8.0 was added to the well followed by 0.25 mL of fluorescamine in acetone (Sigma, 30 mg·100 mL^{-1}). Plates were read on the fluorometer 5 min after fluorescamine addition with 340 nm excitation and 460 nm emission filters.

Median effective doses (ED50s) for the extract dilution curves and dioxin standard curves were determined by fitting a logistic function to the data:

$$[1] \qquad \text{EROD} = \text{BACKGROUND} + \frac{ERODMAX - BACKGROUND}{1 + e^{\gamma(\log(ED50) - \log(DOSE))}}$$

where EROD is the measured EROD activity of each replicate in picomoles per milligram protein per minute, BACKGROUND is the mean activity of the DMSO blanks, γ is a slope parameter, and ERODMAX is the plateau of activity reached by the cells. DOSE is the dose given to the cells in units of picograms per well for dioxin standards or dilution fraction (given that the most concentrated extract has a dilution of 1 for the liver extracts). Toxic equivalent concentrations (TECs) of 2,3,7,8-TCDD in picograms per gram were derived from the ratio of 2,3,7,8-TCDD standard curve ED50s to sample extract ED50s as described by Tillitt et al. (1990). The assay was sensitive to 0.5 pg·g^{-1}. Mean liver lipid levels for all groups analyzed for bioassay-derived TECs ranged between 7.1 and 10.4%. Since there were no significant between group differences in lipid levels, samples were not corrected for lipid content.

Chlorinated dioxin/furan, water chemistry, and extractable organic chloride analysis

Individual livers from six Sawmill Creek male sucker and three Mountain Bay sucker were collected at 0 d for PCDD and PCDF analysis. One pooled sample from each of the Mountain Bay and Jackfish Bay 8-d plume-exposed fish were prepared for dioxin and furan analysis. Individual livers were minced and 1.0 g was removed and added to the pooled sample. Thus, the pooled samples consisted of equal amounts of liver from each of the ten 8 d exposed fish in each group.

Liver samples for congener-specific dioxin and furan analyses were analyzed according to Huestis and Sergeant (1992). Liver was ground in sodium sulphate, placed in glass columns, spiked with a mixture of ^{13}C dioxin and furan congeners, and extracted with methylene chloride. The resulting extract was cleaned up by automated GPC followed by alumina chromatography. A final cleanup using carbon fibre chromatography isolated the planar compounds. Samples were quantified using gas chromatography with high resolution mass-spectroscopy detection (VG Autospec). Concentrations were corrected for the recovery of the ^{13}C labelled congeners.

Estimates of pulp mill effluent exposure of sucker caged in the plume water were determined using adsorbable organic halogen (AOX), free chloride, and free sodium measured in undiluted effluent, as well as near the site of experimental caging. AOX determination was performed by a carbon adsorption combustion microcoulometric method using a Dohrmann AOX analyzer at the Wastewater Technology Centre, Burlington, Ont. Sodium and chloride were measured according to the methods of the Environment Canada National Water Quality Laboratory (Burlington, Ont., Canada).

Table 2. Toxic equivalent factors for selected polychlorinated dibenzo-*p*-dioxins[a] and dibenzofurans derived for H4IIE cell line.

Congener[a]	H4IIE-TEF
Dioxins	
2,3,7,8-TCDD	1.0
1,2,3,7,8-PCDD	1.13[b]
1,2,3,4,7,8-HCDD	0.49[b]
1,2,3,6,7,8-HCDD	0.23[b]
1,2,3,7,8,9-HCDD	0.01[c]
1,2,3,4,6,7,8-HpCDD	0.097[b]
Furans	
2,3,7,8-TCDF	0.030[b]
1,2,3,7,8-PCDF	0.16[b]
2,3,4,7,8-PCDF	0.40[b]
1,2,3,4,7,8-HCDF	0.33[b]
2,3,4,6,7,8-HCDF	0.2[c]
1,2,3,6,7,8-HCDF	0.1[c]
1,2,3,7,8,9-HCDF	0.01[c]
1,2,3,4,6,7,8-HpCDF	0.01[c]

[a]Abbreviations for PCDDs and PCDFs; T, tetra; P, penta; H, hexa; Hp, hepta; O, octa.
[b]H4IIE TEFs generated using current methodology (Clemons et al. 1994).
[c]H4IIE TEFs previously published (Safe 1987).

Table 3. Measured mean (SE) whole-fish parameters of white sucker captured at Jackfish Bay (BKME exposed) (n = 73) and Mountain Bay (reference) (n = 76). For liver EOCl, n = 24 for Jackfish and n = 20 for Mountain.

Parameter	Jackfish	Mountain
Length (cm)	38.0 (0.3)***	39.4 (0.2)
Weight (g)	769.4 (17.3)	789.5 (10.9)
Condition factor	1.39 (0.01)***	1.28 (0.01)
GSI	4.17 (0.10)***	4.77 (0.90)
LSI	1.43 (0.30)***	1.61 (0.31)
Age (year)	11.0 (0.3)*	10.1 (0.2)
Liver EOCl $\mu g \cdot g^{-1}$	30.1 (5.0)***	3.8 (0.8)

*$p < 0.05$
***$p < 0.001$

To determine what fraction of the Sawmill Creek fish were exposed to mill effluent, extractable organic chloride (EOCl) was examined in muscle tissue of prespawning male white sucker. Tissue was ground and extracted in a 1:1 mixture of isopropanol:cyclohexane. After centrifugation the supernatant was washed with 50 mL of 0.01 N H_2SO_4 and extracted twice with 100 mL of cyclohexane. The resulting organic phase was evaporated to 0.5 mL. Chlorine content of these extracts was measured by neutron activation by the Saskatchewan Research Council (Saskatoon, Sask.).

Calculation of TECs from dioxin and furan residue data

Dioxin and furan congeners were measured in individual samples from 0-d prespawning sucker and in pooled samples from the 8-d plume caging with Mountain Bay and Sawmill Creek fish. Calculated TECs were derived from those chemical residues by multiplying the molar concentration of each congener by its molar potency ratio or toxic equivalent factor (TEF; Table 2) and summing the contribution of all of the measured congeners. To facilitate direct comparison with the H4IIE bioassay-derived TECs, TEFs were experimentally derived for a series of PCDD and PCDF congeners as described in Clemons et al. (1994). Values for congeners not tested by Clemons et al. (1994) were taken from the H4IIE-derived values of Safe (1987).

Statistics

Nonlinear curve fitting of dose–effect curves was performed using a SYSTAT version 5.0 (Wilkinson 1990) basic program (MACRO), which utilized the NONLIN module for curve fitting. Correlations of measured parameters were assessed using Pearson correlation coefficients in conjunction with corresponding probabilities to determine the statistical significance of each correlation (CORR module). Length, weight, GSI, and LSI data were tested by one-way ANOVA. Condition factor was tested using analysis of covariance (ANCOVA) and age was tested using Kruskal–Wallis nonparametric analysis of variance. The statistical significance of all other data was tested using ANOVA with either Dunnett's test (all treatments vs. one control) or Tukey's test (all possible pairwise comparisons). Data homoscedasticity was tested using Barlett's test. Normality was examined using probability plots. Heteroscedastic or non-normal data were log transformed and retested prior to performing statistical tests requiring that these assumptions be met. Statistical significance was assessed at $\alpha = 0.05$.

Results

Prespawning male white sucker collected at Jackfish Bay were significantly shorter than those collected at Mountain Bay (Table 3, $p < 0.001$), but there was no significant difference in weight between fish from the two sites. This resulted in a higher condition factor for Jackfish Bay fish ($p < 0.001$). Age of fish was also significantly different, with the Mountain Bay fish being, on average, 1 year younger than the Jackfish Bay sucker ($p = 0.032$). The Jackfish Bay sucker had both smaller gonads per body weight (GSI, $p < 0.001$) and smaller livers per body weight (LSI, $p < 0.001$).

Muscle EOCl in Jackfish Bay white sucker was eightfold higher than levels measured in Mountain Bay sucker. Examination of these data (Fig. 2) indicates that 15–20% of the Sawmill Creek sucker had levels of EOCl comparable with Mountain Bay sucker; it follows that at least 80% of the Sawmill Creek sucker had recently been exposed to BKME. Sucker caged in the Jackfish Bay receiving area were exposed to about a 40–50% dilution of the mill effluent according to AOX, Na^+ and Cl^- measurements taken over the course of the caging period (Table 4).

Fig. 2. White sucker liver extractable organic chloride (EOCl) frequency distribution for fish captured at Sawmill Creek (JFB) and the Little Gravel River (MTN).

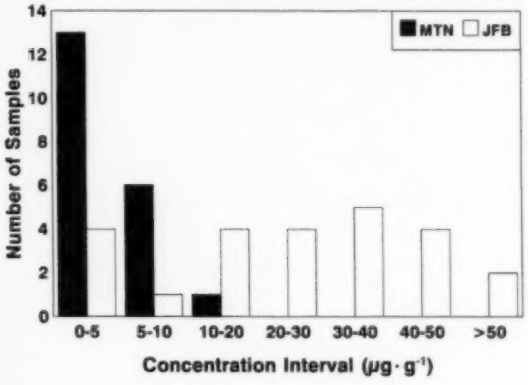


Table 4. Measured mean (SE) chemical parameters for undiluted mill effluent and receiving water at the mouth of Blackbird creek.

Measurement	Caging area concentration ($mg \cdot L^{-1}$)[a]	Effluent concentration ($mg \cdot L^{-1}$)[b]	Dilution (%)
AOX	7.55 (0.41)	16.00 (0.48)	47.2
Cl^-	186.1 (3.8)	411.3 (2.6)	45.3
Na^+	140.8 (5.0)	342.0 (2.6)	41.1

[a] $n = 6$.
[b] $n = 3$.

There was no significant difference between sites in liver EROD activity of the 0-d male prespawning white sucker (Fig. 3). No site-related differences were seen in the 4-d caging controls or the 21-d controls. When all three control groups of control fish were pooled, there were still no significant EROD differences between sites. Exposure of Jackfish Bay and Mountain Bay fish to the BKME effluent plume resulted in a rapid induction of hepatic EROD levels with induction ranging from 10- to 30-fold. There were no clear differences in induction between 2, 4, and 8-d. All data were highly variable, some fish showing no increases in EROD activity while the majority showed moderate to high levels. There were significant EROD elevations in all of the plume-exposed groups as compared with control groups ($p < 0.01$). The highest dose of the positive control (β-NF exposure; Fig. 4) induced liver EROD 15-fold. There was a dose-related trend in the EROD values of the positive controls. However, only the Mountain 5 and 50 $mg \cdot kg^{-1}$ and the Jackfish 50 $mg \cdot kg^{-1}$ doses of β-NF were significantly elevated over their respective 4-d caged controls.

Samples of liver from Jackfish Bay sucker had higher levels of TECs calculated from PCDDs and PCDFs than did samples from Mountain Bay fish (Table 5). This was largely due to higher levels of 2,3,7,8-TCDD and 2,3,7,8-TCDF that were 24- and 23-fold higher than the Mountain Bay samples, respectively. Comparison of 0-d TECs calculated from PCDD and PCDF residues with TECs from the 8-d plume-exposed pooled sample show that there was no increase in the calculated TECs of the Jackfish Bay sucker, and only a marginal increase (0.2 $pg \cdot g^{-1}$) in the Mountain Bay TECs. Thus, there were no apparent increases in the calculated biological potency of PCDDs and PCDFs with 8 d exposure to effluent.

Fig. 3. Hepatic 7-ethoxyresorufin-*O*-deethylase (EROD) activity in white sucker exposed to a BKME plume and caged in clean water (control). Concentrations in all plume-exposed groups are significantly higher than in all control groups ($p < 0.01$ for all). There were no significant differences with control groups or within plume exposed groups. Error bars indicate SE. $n = 10$ for all but 0 d where $n = 20$ and 21 d where $n = 6$.

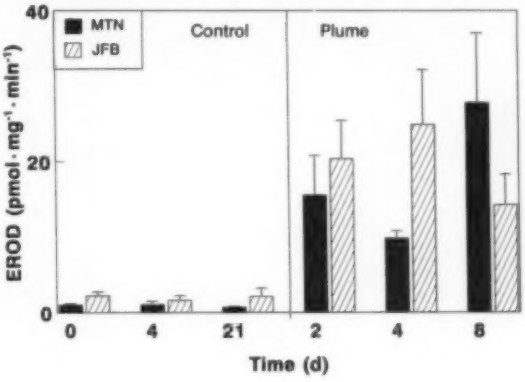


Fig. 4. Hepatic 7-ethoxyresorufin-*O*-deethylase (EROD) activity in white sucker injected intraperitoneally with β-naphthoflavone suspended in triolein carrier after 4 d. Control represents 4-d caged control fish. Error bars indicate SE. Carrier fish were injected with triolein only. Asterisks indicate significant differences between control and treatments in Mountain Bay fish; crosses indicate differences between control and treatments in Jackfish Bay fish. $n = 10$ for control bars, $n = 4$ for all other bars; *, $p < 0.05$; ***, $p < 0.001$.

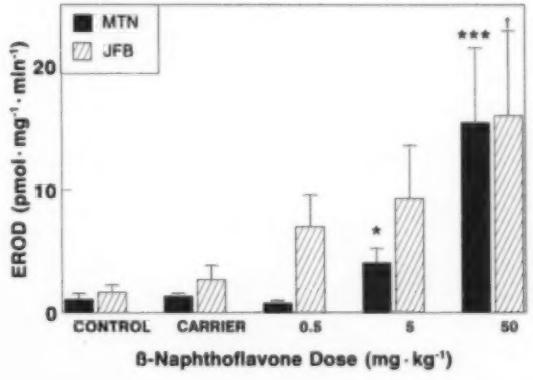


Table 5. Measured mean (SE) PCDDs, PCDFs, and toxic equivalent concentrations (TECs) in samples of liver from white sucker captured during spawning migration (0 d) or exposed to the Jackfish Bay BKME receiving area water for 8d.

	Jackfish Bay ($pg \cdot g^{-1}$)		Mountain Bay ($pg \cdot g^{-1}$)	
Congener	Day 0	Day 8	Day 0	Day 8
2,3,7,8-TCDD	19.5 (7.1)	11.1	0.81 (0.81)	1.0
1,2,3,7,8-PCDD	ND[a]	2.3	ND	<2.2
1,2,3,4,7,8-HCDD	0.26 (0.25)	1.0	ND	<1.0
1,2,3,6,7,8-HCDD	0.26 (0.26)	1.2	0.81 (0.81)	<0.9
1,2,3,7,8,9-HCDD	0.20 (0.20)	0.9	ND	<1.0
1,2,3,4,6,7,8-HpCDD	2.79 (1.49)	3.2	3.57 (2.11)	3.0
OCDD	3.42 (1.72)	9.6	10.2 (3.4)	104.1
2,3,7,8-TCDF	139.9 (66.3)	74.7	6.18 (3.09)	10.7
1,2,3,7,8-PCDF	0.78 (0.78)	3.6	ND	<2.5
2,3,4,7,8-PCDF	ND	<1.4	ND	<3.6
1,2,3,4,7,8-HCDF	0.15 (0.15)	2.1	0.37 (0.36)	<0.7
2,3,4,6,7,8-HCDF	ND	1.0	ND	<0.6
1,2,3,6,7,8-HCDF	ND	1.0	ND	<0.7
1,2,3,7,8,9-HCDF	ND	0.8	0.43 (0.43)	<0.7
1,2,3,4,6,7,8-HpCDF	0.14 (0.14)	1.7	0.31 (0.31)	1.7
OCDF	2.16 (1.48)	2.6	1.01 (1.01)	2.6
Toxic equivalent concentrations				
(PCDD/PCDF) calculated TEC	24.3	18.7	1.4	1.6
Bioassay-derived TEC	31.0 (5.7)[b]	56.2 (10.4)	4.6 (1.1)[b]	35.8 (4.6)

Note: Day 8 samples represent one analysis of a sample of 10 pooled livers ($n = 6$ individual livers for day-0 Jackfish Bay; $n = 3$ for day-0 Mountain Bay, $n = 10$ for bioassay derived TECs).

[a]ND, not detected.

[b]These bioassay-derived TECs are for 4-d caging controls, not 0-d controls.

H4IIE bioassay-derived TECs showed that the Jackfish sucker had significantly higher levels of EROD-inducing compound present in the liver tissue than did the Mountain Bay males at all time periods ($p < 0.001$; Fig. 5). The Mountain Bay plume caged fish showed significant increases in liver TECs over the 4 and 21d controls ($p < 0.001$), while the Jackfish Bay sucker showed no statistically significant changes between any of the treatments. Correlations of bioassay-derived TECs with liver EROD on an individual fish basis showed a significant correlation for Mountain Bay fish ($r = 0.347$, $p = 0.018$) and no significant correlation for Jackfish Bay fish.

A comparison of the H4IIE bioassay-derived TECs for the 8-d plume-exposed fish to those calculated from the congener specific PCDD and PCDF data revealed that the PCDD/PCDF-derived TECs accounted for only 32.4 and 4.3% of the H4IIE bioassay-derived TECs in the Jackfish Bay and Mountain Bay groups, respectively (Table 5). However, comparison of TECs from PCDD and PCDF data for four Jackfish Bay fish sampled at 0 d with the mean bioassay-derived TEC of the 4-d Jackfish Bay cage controls indicated that 83% of the bioassay-derived TECs could be accounted for by PCDDs and PCDFs.

Plasma steroid hormones 11-ketotestosterone and testosterone showed a significant (Fig. 6; $p < 0.01$) initial difference between sites with the Mountain Bay sucker having lower levels of both hormones. Upon caging, the levels of both hormones showed similar changes, with declines approaching two orders of magnitude within 2 d of capture. The 4-d caging controls also showed large drops although they remained significantly higher than sucker exposed to the plume for 4 d. The Jackfish Bay caging control sucker did not experience as severe a drop in plasma steroid levels as did the Mountain Bay caging controls.

Discussion

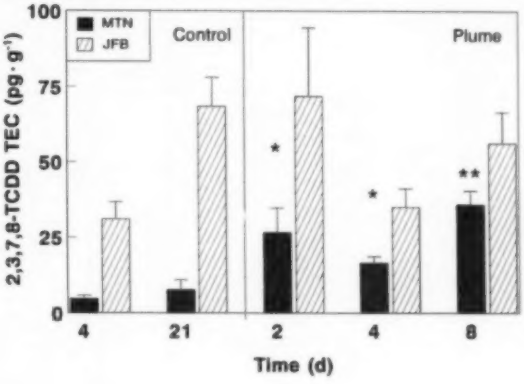
The results of the present study have demonstrated that P4501A induction in fish exposed to BKME was likely caused by a family of compounds other than PCDDs and PCDFs. Fish previously exposed to BKME had significantly higher H4IIE bioassay-derived TECs and PCDD/PCDF-derived TECs than did reference fish but did not show elevated MFO induction. Induction of the hepatic MFO enzyme P4501A occurred 2 d after experimental exposure to the BKME effluent plume. Since changes in EROD induction did not correspond with increases in PCDD/PCDF-derived TECs but did correlate with increases in bioassay-derived TECs, it appears that MFO-inducing compounds of unknown identity are present in the liver tissue while PCDDs and PCDFs residues apparently had no detectable enzyme-inducing effect.

Physiological parameters measured in white sucker showed similar trends as compared with previous years, whereas biochemical measurements did not. Male sucker had significantly lower gonad to body weight ratios and higher condition factors resulting from a length difference, similar to previous studies (McMaster et al. 1991; Munkittrick et al. 1991). Prespawning male white sucker from Jackfish Bay demonstrated no significant difference in 0-d hepatic EROD activity when compared with fish from Mountain Bay. Prespawning male white sucker from Jackfish Bay have shown significant MFO induction in 1989 (McMaster et al 1991), 1990–1992 (Munkittrick et al. unpublished data), but not in 1988 (Munkittrick et al. 1991). In previous years, both testosterone and 11-ketotestosterone concentrations from Jackfish Bay sucker were significantly lower than those in fish from the reference site (McMaster et al. 1991; Van Der Kraak et al. 1992). The steroid reversal observed this year cannot be easily interpreted because the reference fish were transported for 1 h before blood was removed, and the Sawmill Creek fish were not. Both transportation and holding stress have been shown to depress steroid hormone concentrations within 1 h (McMaster et al. 1994; J. Jardine, K.R. Munkittrick, and G. Van Der Kraak, unpublished data). Year to year differences in spring biochemical measurements may be due to the length of time that Jackfish Bay fish spend in clean water prior to spawning. The BKME-exposed site is several kilometres from the spawning stream and the duration of the residence in clean water prior to spawning has not been determined. Induction of hepatic MFO activity and reduction of plasma steroid hormones appear to respond and recover rapidly to the influence of BKME exposure (Munkittrick et al. 1992, 1995).

Differences between the absolute levels of MFO induction between spring and fall are not likely due to the influence of steroid hormones on the expression of P4501A. Levels of MFO induction in spring-captured males have in the past been approximately three-fold higher than those in fish from the reference site. In summer and fall samplings typically a 20-fold MFO induction has been observed (McMaster et al. 1991; Munkittrick et al. 1991). The seasonal differences in MFO induction have previously been attributed to elevated levels of reproductive hormones, or a related factor, during the spawning period. In this study, sucker injected with β-NF and sucker exposed to the effluent plume were clearly capable of induction up to 20-fold. The induction in the plume-caged fish cannot be attributed to the drop in androgens alone since fish caged in clean water for 4 and 21-d did not show any indication of an increase in EROD activity despite similar drops in steroid hormone concentrations. Although steroids were not measured in the 21-d fish, these can be assumed to be very low since the testes, which synthesize these androgens, had atrophied and were being resorbed.

The induction of liver MFO activity was not paralleled by the bioconcentration of TECs calculated from PCDDs and PCDFs. Comparison of 0-d TECs calculated from PCDDs and PCDFs to TECs measured in sucker exposed to the plume for 8 d demonstrated that PCDD/PCDF-derived TECs did not appear to accumulate in the liver

Fig. 5. H4IIE bioassay-derived 2,3,7,8-tetrachlorodibenzo-*p*-dioxin toxic equivalent concentration (TEC) in the livers of white sucker exposed to a bleached kraft mill receiving area. Jackfish Bay TECs are significantly different than Mountain Bay TECs at all time periods shown. Asterisks indicate significant differences between Mountain Bay plume-exposed fish and Mountain Bay 4-d caged controls; *, $p < 0.05$; **, $p < 0.01$. Error bars indicate SE. $n = 10$ for all groups except 21 d where $n = 6$.

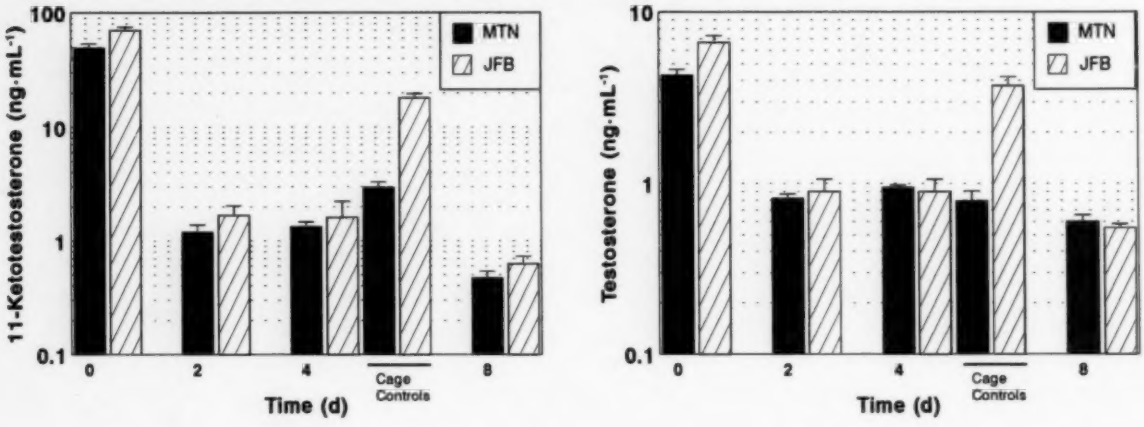


tissue over the caging period. The threshold liver concentration for MFO induction in rainbow trout was observed to be 20 $pg \cdot g^{-1}$ of 2,3,7,8-TCDD 7 d after a single oral dose (Parrott 1993). The PCDD/PCDF-derived liver TECs in Mountain Bay fish were more than an order of magnitude lower than this even after an 8-d plume exposure. Changes in mill processes designed to reduce the output of chlorinated organics have reduced effluent concentrations of PCDDs and PCDFs to nondetectable levels at this mill (Karl 1992). Thus, it is unlikely that biologically significant levels of PCDDs and PCDFs could be accumulated from short-term exposure to the water column; our results support this hypothesis.

Prior to experimental caging, there was no site-related difference in MFO activity despite significant site differences in both TECs derived from PCDDs and PCDFs as well as bioassay-derived TECs. Jackfish Bay prespawning fish had 10-fold higher bioassay-derived TECs than the Mountain Bay fish yet there was no significant EROD induction in Jackfish Bay fish. In Jackfish Bay sucker, both PCDD/PCDF-based as well as bioassay-derived TECs exceeded the threshold liver concentration of 20 $pg \cdot g^{-1}$ observed in rainbow trout (Parrott 1993). It appears that the dioxin and furan residues stored in the liver tissue were not biologically active at this time, or were not present in sufficient concentration to cause MFO induction in white sucker. These PCDD and PCDF residues were likely not bioavailable within the tissues of the fish due to storage in lipid.

TECs calculated from PCDD and PCDF residues cannot account for the increases that occurred in the H4IIE bioassay-derived TECs in Mountain Bay fish exposed to BKME. This indicates that the accumulation of compounds that induce EROD in H4IIE cells, and were not PCDDs or

Fig. 6. Plasma concentrations of 11-ketotestosterone and testosterone in white sucker caged in a BKME plume. At 0 d Jackfish Bay fish had significantly higher levels of both testosterone and 11-ketotestosterone than Mountain Bay sucker. All subsequent treatments are significantly lower than the 0-d values. Error bars indicate SE. $n = 10$ for all bars.



PCDFs, was detectable in the Mountain Bay fish. An increase in bioassay-derived TECs was likely not detectable in the Jackfish Bay BKME-caged fish because of the variability caused by the already high levels of bioassay-derived TECs in this tissue. Our findings strongly support recent experimental evidence suggesting that PCDDs and PCDFs may not be the main MFO inducers in BKME (Munkittrick et al. 1992, 1995).

Contrary to past observations (van den Heuvel, 1994), only 32.4% of the TECs in 8-d plume-exposed Jackfish Bay fish could be accounted for due to TECs calculated from PCDDs and PCDFs. Although there was no significant increase in bioassay-derived TECs upon plume exposure, the Jackfish Bay sucker exposed to the plume for 8 d had 30% higher TECs than the 4-d caging controls. The difference between this result and that of the previous study may be due to non-PCDD/PCDF MFO-inducing compounds taken up during the 8-d exposure. This explanation is supported by a comparison of bioassay-derived TECs in the 4-d caging controls with 0-d PCDD/PCDF-calculated TEC measurements for Jackfish Bay fish. Although these measurements were performed on different fish samples, these data indicate that nearly all (83%) of the bioassay-derived TECs can be accounted for by PCDDs and PCDFs.

The tissue cleanup technique used in this work allowed the unknown MFO-inducing compounds that accumulated in sucker liver to be detected using the H4IIE bioassay. This method was chosen to allow a broad spectrum of low molecular weight compounds to pass through to the final extract. Recoveries for PCDDs, PCDFs, and PCBs were excellent; PAH and β-NF recoveries were variable. The relatively stable and nonvolatile MFO-inducing PAHs (benzo[a]pyrene, chrysene and 3-methylcholanthrene) showed >90% recovery. Reasons for the poor recovery of β-NF, naphthalene, and dibenzo[*a*,*i*]pyrene are not known. Understanding the limitations of the cleanup technique is essential, since it appears that compounds responsible for the MFO induction observed in fish exposed to pulp mill effluent have not been fully characterized.

The MFO-inducing compounds detected by the H4IIE bioassay in white sucker liver tissue remain unidentified. Judging by past and present experimental evidence, this compound or these compounds are relatively water soluble as compared with PCDDs and PCDFs, are potent MFO inducers, and are rapidly metabolized and excreted. This description fits the profile of a PAH-type compound. Lower chlorinated dioxins and furans or diphenyl ethers are also possibilities, but these compounds have not been observed to be potent MFO inducers. Several novel PAHs have recently been characterized in BKME (Koistinen et al. 1994*a*; 1994*b*).

There is still limited knowledge on the biological activity of specific chemicals present in pulp mill effluent. Public perception and legislative changes have focused on organochlorine contaminants because some of them are highly toxic and persistent in the environment, particularly the infamous chlorinated dioxins and furans. This work indicates that some preconceived ideas regarding the causative agents of the effects of pulp mill effluent on fish may not be correct at the sites that we have examined. Further research will combine in vitro bioassays with more detailed chemical fractionation and characterization.

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References

Adams, S.M., W.D. Crumby, M.S. Greeley, L.R. Shugart, and C.F. Saylor. 1992. Responses of fish populations and communities to pulp mill effluents: a holistic assessment. Ecotoxicol. Environ. Saf. 24: 347–360.

Andersson, T., L. Förlin, J. Härdig, and Å. Larsson. 1988. Physiological disturbances in fish living in coastal water polluted with bleached kraft pulp mill effluents. Can. J. Fish. Aquat. Sci. 45: 1525–1536.

Bookstaff, R.C., F. Kamel, R.W. Moore, D.L. Bjerke, and R.E. Peterson. 1990. Altered regulation of pituitary gonadotropin-releasing hormone (GnRH) receptor number and pituitary responsiveness to GnRH in 2,3,7,8,-tetrachlorodibenzo-*p*-dioxin-treated male rats. Toxicol. Appl. Pharmacol. 105: 78–92.

Bradford, M.M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem. 72: 248–254.

Clemons, J.H, M.R. van den Heuvel, J.J. Stegeman, D.G. Dixon, and N.C. Bols. 1994. A comparison of toxic equivalent factors for selected dioxins and furans congeners derived using fish and mammalian cell lines. Can. J. Fish. Aquat. Sci. 51: 1577–1584.

Courtenay, S., C. Grunwald, G.L. Kreamer, R. Alexander, and I. Wirgin. 1993. Induction and clearance of cytochrome P4501A mRNA in Atlantic tomcod caged in bleached kraft mill effluent in the Miramichi River. Aquat. Toxicol. 27: 225–243.

Goldstein J.A. and S. Safe. 1989. Mechanism of action and structure-activity relationships for the chlorinated dibenzo-*p*-dioxins and related compounds, p. 239–293 *In* Kimbrough and Jensen [ed.] Halogenated biphenyls, terphenyls, naphthalenes, dibenzodioxins and related products. 2nd ed. Elsevier Science Publishers, Amsterdam.

Hahn, M.E. and J.J. Stegeman. 1992. Phylogenetic distribution of the Ah receptor in non-mammalian species: implications for dioxin toxicity and Ah receptor evolution. Chemosphere, 25: 931–937.

Hodson, P.V., M. McWhirter, K. Ralph, B. Gray, D. Thivierge, J.H. Carey, G. Van Der Kraak, D.M. Whittle, and M.C. Levesque. 1992. Effects of bleached kraft mill effluent on fish in the St. Maurice River, Quebec. Environ. Toxicol. Chem. 11: 1635–1651.

Huestis, S.Y., and D.B. Sergeant. 1992. Removal of chlorinated diphenyl ether interferences for analyses of PCDDs and PCDFs in fish. Chemosphere, 24: 537–545.

Karås, P., E. Neuman, and O. Sandström. 1991. Effects of a pulp mill effluent on the population dynamics of perch, *Perca fluviatilis*. Can. J. Fish. Aquat. Sci 48: 28–34.

Karl, W. 1992. The new Terrace Bay. Kimberly-Clark turns over a new leaf at Ontario Mill. Pulp Paper J. 91: 43–46.

Koistinen, J., J. Paasivirta, T. Nevalainen, and M. Lahtipera, 1994*a*. Chlorophenanthrenes, alkylchlorophenanthrenes and alkylchloronaphthalenes in kraft pulp mill products and discharges. Chemosphere, 28: 1261–1277.

Koistinen, J., J. Paasivirta, T. Nevalainen, and M. Lahtipera, 1994*b*. Chlorinated fluorenes and alkylfluorenes in bleached kraft pulp and pulp mill discharges. Chemosphere, 28: 2139–2150.

Lindström-Seppä, P., and A. Oikari. 1990. Biotransformation activities of feral fish in waters receiving bleached pulp mill effluents. Environ. Toxicol. Chem. 9: 1415–1424.

Lorenzen, A., and S.W. Kennedy. 1993. A fluorescence-based protein assay for use with a microplate reader. Anal. Biochem. 214: 346–348.

Mably, T.A., R.W. Moore, and R.E. Peterson. 1992. *In utero* and lactational exposure of male rats to 2,3,7,8,-tetrachlorodibenzo-*p*-dioxin. 1. Effects on androgenic status. Toxicol. Appl. Pharmacol. 114: 97–107.

McMaster, M.E., G.J. Van Der Kraak, C.B. Portt, K.R. Munkittrick, P.K. Sibley, I.R. Smith, and D.G. Dixon. 1991. Changes in hepatic mixed-function oxygenase (MFO) activity, plasma steroid levels and age at maturity of a white sucker (*Catostomus commersoni*) population exposed to bleached kraft mill effluent. Aquat. Toxicol. 21: 199–218.

McMaster, M.E., C.B. Portt, K.R. Munkittrick, and D.G. Dixon. 1992. Milt characteristics, reproductive performance, and larval survival and development of white sucker exposed to bleached kraft mill effluent. Ecotoxicol. Environ. Saf. 23: 103–117.

McMaster, M.E., K.R. Munkittrick, P.L. Luxon, and G.J. Van Der Kraak. 1994. Impact of low-level sampling stress on interpretation of physiological responses of white sucker exposed to effluent from a bleached kraft pulp mill. Ecotoxicol. Environ. Saf. 27: 251–264.

Moore, R.W., C.R. Jefcoate, and R.E. Peterson. 1991. 2,3,7,8-tetrachlorodibenzo-*p*-dioxin inhibits steroidogenesis in the rat testis by inhibiting the mobilization of cholesterol to cytochrome P450. Toxicol. Appl. Pharmacol. 109: 85–97.

Muir, D.C.G., A.L. Yarechewski, D.A. Metner, W.L. Lockhart, G.R.B. Webster, and K.J. Friesen. 1990. Dietary accumulation and sustained hepatic mixed function oxidase enzyme induction by 2,3,7,8-pentachlorodibenzofuran in rainbow trout. Environ. Toxicol. Chem. 9: 1463–1472.

Munkittrick, K.R., C.B. Portt, G.J. Van Der Kraak, I.R. Smith, and D.A. Rokosh. 1991. Impact of bleached kraft mill effluent on population characteristics, liver MFO activity, and serum steroid levels of a Lake Superior white sucker (*Catostomus commersoni*) population. Can. J. Fish. Aquat. Sci. 48: 1371–1380.

Munkittrick, K.R., M.E. McMaster, C.B. Portt, G.J. Van Der Kraak, I.R. Smith, and D.G. Dixon. 1992*a*. Changes in maturity, plasma sex steroid levels, hepatic mixed function oxygenase activity, and the presence of external lesions in lake whitefish (*Coregonus clupeaformis*) exposed to bleached kraft mill effluent. Can. J. Fish. Aquat. Sci. 49: 1560–1569.

Munkittrick, K.R., G.J. Van Der Kraak, M.E. McMaster, and C.B. Portt. 1992*b*. Response of hepatic MFO activity and plasma sex steroids to secondary treatment of bleached kraft pulp mill effluent and mill shutdown. Environ. Toxicol. Chem.11: 1427–1439.

Munkittrick, K.R., G.J. Van Der Kraak, M.E. McMaster, C.B. Portt, M.R. van den Heuvel, and M.R. Servos. 1994. Survey of receiving water environmental impacts associated with discharges from pulp mills. II. Gonad size, liver size, hepatic MFO activity and plasma steroid levels in white sucker. Environ. Toxicol. Chem. 13: 1089–1101.

Munkittrick, K.R., M.R. Servos, K. Gorman, B. Blunt, M.E. McMaster, and G.J. Van Der Kraak. 1995. Characteristics of EROD induction associated with exposure to pulp mill effluent. *In* T.W. LaPointe, F.T. Price, and E.E. Little [ed.] Environmental toxicology and risk assessment. 4. American Society for Testing and Materials, Philadelphia, Pa. In press.

Nebert, D.W., D.D. Peterson, and A.J. Fornace, Jr. 1990. Cellular responses to oxidative stress: the (Ah) gene battery as a paradigm. Environ. Health Perspect. 88: 13–25.

Opperhuizen, A., and D.T.H.M. Sijm. 1990. Bioaccumulation and biotransformation of polychlorinated dibenzo-*p*-dioxins and dibenzofurans in fish. Environ. Toxicol. Chem. 9: 175–186.

Parrott, J.L. 1993. Relative potency of polychlorinated dibenzo-*p*-dioxins and dibenzofurans for inducing MFO activity in

rainbow trout. Ph.D. thesis, University of Waterloo, Waterloo, Ont.

Pohl, R.J., and J.R. Fouts. 1980. A rapid method for assaying the metabolism of 7-ethoxyresorufin by microsomal subcellular fractions. Anal. Biochem. 107: 150–155.

Rogers, I.H., C.D. Levings, W.L. Lockhart, and R.J. Norstrom. 1989. Observations on overwintering juvenile chinook salmon (*Oncorhynchus tshawytscha*) exposed to bleached kraft mill effluent in the upper Fraser River, British Columbia. Chemosphere, 19: 1853–1868.

Safe, S. 1987. Determination of 2,3,7,8-TCDD toxic equivalent factors (TEFs): support for the use of the in vitro AHH induction assay. Chemosphere, 16: 791–802.

Servizi, J.A., R.W. Gordon, D.W. Martens, W.L. Lockhart, D.A. Metner, I.H. Rogers, J.R. McBride, and R.J. Norstrom. 1993. Effects of biotreated bleached kraft mill effluent on fingerling chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 50: 846–857.

Servos, M.R., S. Huestis, D.M. Whittle, and K.R. Munkittrick. 1994. Survey of receiving water environmental impacts associated with discharges form pulp mills III. Levels of dioxins and furans in muscle and liver as measured by GC/MS. Environ. Toxicol. Chem. 13: 1103–1115.

Smith, I.R., C.B. Portt, and D.A. Rokosh. 1991. Hepatic mixed function oxidases induced in populations of white sucker, (*Catostomus commersoni*), from areas of Lake Superior and the St. Marys River. J. Great Lakes Res. 17: 382–393.

Tillitt, D.E., J.P. Giesy, and G.T. Ankley. 1990. Characterization of the H4IIE rat hepatoma cell bioassay as a tool for assessing toxic potency of planar halogenated hydrocarbons in environmental samples. Environ. Sci. Technol. 25: 87–92.

Tillitt, D.E., G.T. Ankley, D.A. Verbrugge, J.P. Giesy, J.P. Ludwig, and T.J. Kubiak. 1991. H4IIE rat hepatoma cell bioassay-derived 2,3,7,8-tetrachlorodibenzo-*p*-dioxin equivalents in colonial fish-eating waterbird eggs from the Great Lakes. Arch. Environ. Contam. Toxicol. 21: 91–101.

van den Heuvel, M.R. K.R. Munkittrick, G.J. Van Der Kraak, M.E., McMaster, C.B. Portt, M.R. Servos, and D.G. Dixon. 1994. Survey of receiving water environmental impacts associated with discharges from pulp mills. IV. Bioassay derived 2,3,7,8-tetrachlorodibenzo-*p*-dioxin toxic equivalent concentration in white sucker (*Catostomus commersoni*) in relation to biochemical indicators of impact. Environ. Toxicol. Chem. 13: 1117–1126.

Van Der Kraak, G., H.M. Dye, and E.M. Donaldson. 1984. Effects of LH-RH and Des-Gly^{10}(D-Ala)LH-RH-ethylamide on plasma sex steroid profiles in adult female coho salmon (*Oncorhynchus kisutch*). Gen. Comp. Endocrinol. 55: 36–45.

Van Der Kraak, G., P.M. Rosenblum, and R.E. Peter. 1990. Growth hormone-dependent potentiation of gonadotropin-stimulated steroid production by ovarian follicles of the goldfish. Gen. Comp. Endocrinol. 79: 233-239.

Van Der Kraak, G.J., K.R. Munkittrick, M.E. McMaster, C.B. Portt, and J.P. Chang. 1992. Exposure to bleached kraft pulp mill effluent disrupts the pituitary–gonadal axis of white sucker a multiple sites. Toxicol. Appl. Pharmacol. 115: 224–233.

van der Weiden, M.E.J., J. van der Kolk, R. Bleumink, W. Seinen, and M. van den Berg. 1992. Concurrence of P450-1A1 induction and toxic effects after administration of a low dose of 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) in the rainbow trout (*Oncorhynchus mykiss*). Aquat. Toxicol. 24: 123–142.

Wade, M.G., and G. Van Der Kraak. 1991. The control of testicular steroidogenesis in the goldfish: effects of activators of different intracellular signalling pathways. Gen. Comp. Endorinol. 83: 337–344.

Wilkinson, L. 1990. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Ill.

A size and age-structured model of the European eel (*Anguilla anguilla* L.)

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Abstract: The life cycle of the European eel (*Anguilla anguilla*) presents several distinctive features, such as high plasticity in body growth, marked sexual dimorphism, sex ratio strongly skewed in favor of females and sexual maturation largely dependent upon the size of individuals. A demographic model incorporating all these characteristics is derived on the basis of a multiple classification of individuals by age and size, and variability in individual growth is explicitly included. Existing theory for size-structured stocks is extended to include the dependence of sexual maturation on size, while natural mortality is age specific. Using 1989 population data from Comacchio lagoons (Italy), we estimate mortality and metamorphosis rate and abundance in each age- and size-class for both yellow and silver eels, crucial information for the management of the Comacchio fishery. The use of a nonparametric technique (bootstrapping) yields not only the moments, but also the distributions of these estimates. Validation of the model is performed on the data collected in 1990. The approach adopted is very flexible and different assumptions about survival, sexual maturation, and net selectivity can be easily incorporated in the model.

Résumé : Le cycle vital de l'anguille européenne (*Anguilla anguilla*) présente plusieurs caractéristiques particulières, notamment une croissance corporelle très plastique, un dimorphisme sexuel marqué, un rapport des sexes qui penche fortement en faveur des femelles et enfin une maturation sexuelle qui dépend étroitement de la taille des individus. Nous avons construit un modèle démographique intégrant toutes ces caractéristiques, à partir d'une classification multiple des individus par âge et par taille, et nous tenons compte de façon explicite de la variabilité dans la croissance individuelle. Nous élargissons la base théorique concernant les stocks à structure de taille pour y faire entrer la dépendance de la maturation sexuelle à l'égard de la taille, tandis que la mortalité naturelle est spécifique à l'âge. À partir de données démographiques recueillies en 1989 dans les lagunes de Comacchio (Italie), nous estimons le taux de mortalité et de métamorphose ainsi que l'abondance dans chaque classe d'âge et de taille, pour les anguilles jaunes et argentées, information qui est cruciale pour la gestion de la pêche de Comacchio. L'emploi d'une technique non paramétrique (amorçage) donne non seulement les moments, mais aussi les distributions de ces estimations. Nous avons validé le modèle avec les données recueillies en 1990. L'approche adoptée est très souple, et il est facile d'intégrer au modèle différentes hypothèses sur la survie, la maturation sexuelle et la sélectivité des filets.

[Traduit par la Rédaction]

Introduction

The most commonly used physiological determinant in structured population models is chronological age. Since their introduction by Leslie (1945), "projection matrices" have been widely used by demographers to describe the dynamics of age-structured populations, primarily because they are relatively easy to construct, analyze, and implement on computers. More recently it has been shown that the use of matrix population models is not restricted to age-structured populations, but can also be applied to those populations whose life cycle is better described in terms of developmental stages or size-classes, rather than age-classes (Lefkovitch 1965; Caswell 1989). In many species the ecological consequences of size on vital parameters (e.g., survivorship, fecundity, sexual maturity) are more important than those due to age. The influence of size is particularly important in organisms with high plasticity in body growth. As Caswell states (1986), size dependence per se does not violate the assumption of classical demography: "if size is closely related to age, then a simple mathematical transformation can express size-dependent vital rates as a function of age." But in many species, variability in growth rate makes age a very poor predictor of size. In these cases models of population dynamics should explicitly include reference to size.

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Kirkpatrick (1984) derived a theory for a size-structured fish stock with variable growth rate and size-dependent mortality. In his paper it is shown how the inclusion of variability in individual growth rate can immensely complicate the construction and the analysis of demographic models. For this reason, size dependence is often ignored in practice, although an extensive literature is now available on the subject (Fournier and Doonan 1987; Schnute 1987; Deriso and Parma 1988; Schnute et al. 1989*a*, 1989*b*).

Here we present a model of the dynamics of European eel (*Anguilla anguilla*) populations. The interest of this study arises from the fact that the life cycle of this catadromous fish is characterized by several distinctive features, such as a marked sexual dimorphism, a sex ratio strongly skewed in favor of females, high plasticity in body growth, commercial exploitation mainly focused on sexually mature eels, and a recruitment of young eels from the sea that is independent of the phenomena occurring in the lagoon environment where the eel spends the adult, prereproductive stage of its life cycle. As a consequence, few studies on population dynamics of the European eel are available (Gatto and Rossi 1979; Vøllestad and Jonsson 1986). In this paper, we focus on the eel populations of the Valli di Comacchio lagoons (northern Italy). This particular case study is used as a practical testing ground in which a hybrid model is derived on the basis of a multiple classification of individuals by age and size. Schnute's (1987) theory is extended to include the dependence of sexual maturation on size, while natural mortality is age specific, as in classical demography. The basis of our formulation is the subdivision of the population into distinct cohorts of individuals. Each cohort is characterized by a continuous distribution of the individuals over a whole range of sizes, this being a feature shared with more complex continuous-time physiologically structured models (Sinko and Streifer 1967; Metz et al. 1986; Banks et al. 1988, 1991). A set of recursive equations specifies, on a discrete-time basis, the demographic fate of the individuals in a cohort according to their age and size distribution. In this sense, the model is somewhat intermediate between classical matrix models and more involved partial differential equation models, combining the computational ease of the former with the flexibility of the latter. Indeed, the model can include a great number of physiological traits that influence reproductive and survival success. Despite the great flexibility in treating a variety of factors involved in the development process of a cohort, from a computational point of view, our formulation is only slightly more complicated than the classical matrix formulation.

In the following, we first review some basic facts about eel biology and the fishing activities that take place at Comacchio, and describe the available data (1989 and 1990). Second, we derive a structured population model through the definition of both population variables and submodels describing body growth, sexual maturation, and survivorship. Third, we illustrate the techniques used to estimate unknown parameters from the 1989 data. Estimation is performed by using an optimization algorithm and nonparametric statistics (bootstrapping). Last, we validate the demographic model using the 1990 data.

Available data for the Comacchio eel fishery

The Valli di Comacchio are three shallow lagoons located in northern Italy (Fig. 1). The overall area is about 10 000 h and mean depth about 1 m; salinity ranges between 20 and 35‰ and water temperature fluctuates between 0 and 30°C during the year. Fishery production of the Valli is based on the natural immigration of many euryhaline species (*Dicentrarchus labrax*, *Sparus aurata*, *Liza saliens*, *Zosterissessor ophiocephalus*, *Platichthys flesus*, *Atherina boyeri*). The European eel, however, constitutes the main yield of Comacchio lagoons, with up to 90% of the annual catch by weight.

After metamorphosis from the glass stage (Tesch 1977), the young eels (elvers) enter the lagoons through sluice gates in late spring and remain in this environment for a variable number of years as yellow eels. Here they feed and grow until they metamorphose into silver eels whereupon the animals migrate to the ocean for spawning. During migration, which occurs mostly between October and December, all silver eels are caught at sluice gates by means of devices called lavorieri, a series of V-shaped screens. The yield of the Valli is, therefore, represented by silver eels; yellow eels are only incidentally caught at the lavorieri. Harvested eel biomass has been recorded since 1781: the average yield was more than 14 kg/ha per year until the mid-1970s, but since then it has declined to much lower figures (mean catch from 1977 to 1991 was ca. 6.15 kg/ha; Table 1). The causes of this decline are various. Between 1978 and 1982 the regional government permitted fishing in the canals that connect the lagoons to the sea during the spring, which is the period of elver recruitment. Other likely causes are insufficient dredging of the same canals and declining water quality resulting from organic pollution.

The Valli di Comacchio lagoons have been extensively studied over the past 20 years (Colombo 1972*a*, 1972*b*; Rossi and Colombo 1976*a*, 1976*b*, 1979; Rossi 1979; Gatto and Rossi 1979; Gatto et al. 1982; Rossi et al. 1986, 1987–1988, 1988; Rossi and Franzoi 1991). The present study is based on sampling carried out by researchers of the Dipartimento di Biologia Evolutiva, University of Ferrara, Ferrara, Italy, between the spring of 1989 and the fall of 1990 (Carrieri et al. 1992), as briefly described below.

The sampling scheme for silver eels takes advantage of the traditional management of the Comacchio fishery. The daily catch is usually held in special tanks kept in water, so that eels can stay alive for several days and sold when the market price reaches its peak. A tank can hold up to 1200–1400 kg, which usually corresponds to a few fishing days. As each tank is weighed, the actual weight of the total autumn catch is known. A number of tanks from different fishing periods were randomly selected for each of the three lagoons and about 50–150 kg of fish were randomly extracted from each selected tank. For each tank, the extracted eels were stratified according to broad size-classes (usually four: (1) <200 g, (2) 200–450 g, (3) 450–650 g, (4) >650 g; see Carrieri et al. 1992 for further details). The strata correspond to different market prices, the price per kilogram being an increasing function of eel size.

A subsample of at least 30–40 specimens was randomly extracted from each stratum, and then each animal was weighed (±5 g) and measured (±5 mm). Stratum-specific weighting factors were computed for each selected tank as the ratio of the biomass (kilograms) in the stratum to the biomass of the corresponding subsample. Two further sets of weighting factors were derived on the basis of the actual catch in different fishing periods within each lagoon and of the overall catch in the three lagoons. Frequency distributions of size were finally obtained by multiplying the eel counts in each size-class by the appropriate weighting factors and then summing across all the fishing periods and lagoons. In 1989, 970 silver eels (486 kg) were extracted according to the scheme described above from 7172 kg taken from the autumn catch at the lavorieri (66 900 kg). The following year, 523 silver eels (284 kg) were extracted from 5603 kg taken from the autumn catch (65 000 kg).

As yellow eels are not commercially fished, 2869 specimens (729 kg) were caught in fyke nets (8-mm mesh size) in the spring of 1989 and a stratified random sample of 791 individuals (175 kg) was extracted. In the spring of 1990, 840 yellow eels (318 kg) were extracted from a 1424 kg sample (Carrieri et al. 1992). Stratification was similar to that for silver eels. The main difference is that the total silver eel population from each lagoon is known, because all of these fish are trapped in the lavorieri, while this is not true for yellows that are not commercially fished. Therefore, the size distribution of yellows was derived by using a set of stratum-specific weighting factors, as for silver eels, and a set of weighting factors proportional to the average catch in fyke nets per day and the area of the three lagoons.

The size structure for yellow and silver eels in 1989 and 1990 is shown in Fig. 2. It should be noted that the size structure of silver eels has a marked bimodal shape (Fig. 2*b*), the smallest silver females being always larger than the largest silver males. Therefore, the fraction of silver females can be easily computed from the normalized size frequency distribution as the histogram area corresponding to typical female sizes (>45 cm). The sex ratio of juvenile yellow eels was derived by inspecting the gonads in a random sample of 57 elvers caught in spring 1989 (M:F = 3:54). Sex was not determined for older yellows and juvenile sex ratio cannot be plainly extended to older age-classes. Age was determined by otolith examination of, respectively, 59 males and 437 females, both yellow and silver, caught between spring 1989 and autumn 1990. It should be noted that age is counted from the date of metamorphosis from the glass to the elver stage. Accordingly, eels sampled in late spring are referred to as being x years old if they have been growing in the yellow stage for x years ($x = 0, 1, 2, \ldots$), whereas x^+ refers to eels caught about 6 months later in the commercial fishery. Total length (l; centimetres) to weight (w; grams) relationships (Table 2) have been computed for both yellow and silver eels. Age–length data are shown in Fig. 3.

In deriving a model of eel population dynamics the following features are taken into account. (*i*) There is a marked sexual dimorphism; females are always larger than males at all ages. (*ii*) The sex ratio is skewed in favor of females that comprise 90% of eels sampled at the silver stage and roughly 95% of eels at the yellow stage. (*iii*) Growth is extremely variable among individuals (Rossi and Colombo 1976*b*), with the size of eels of the same age being scattered over very wide intervals (Fig. 3). (*iv*) A fraction of

Fig. 1. Map of the study area showing the Valli di Comacchio lagoons.

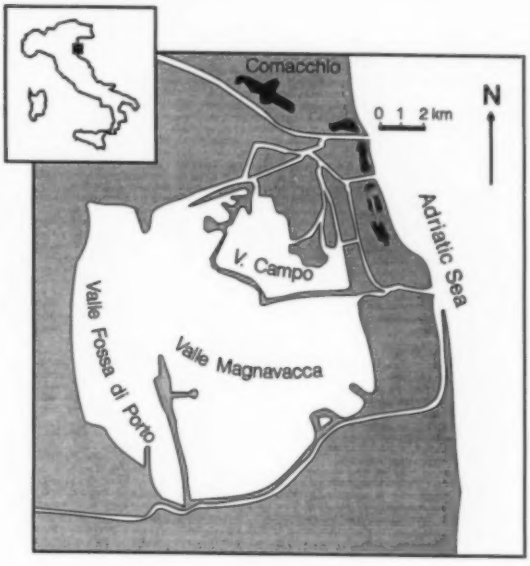


Table 1. Commercial catch of silver eels in the Comacchio lagoon from 1972 to 1991.

Year	Catch (kg)
1972	105 200
1973	156 500
1974	205 400
1975	143 000
1976	116 200
1977	80 200
1978	70 800
1979	66 100
1980	65 000
1981	45 900
1982	43 500
1983	64 600
1984	58 400
1985	35 300
1986	46 000
1987	88 400
1988	87 200
1989	66 900
1990	65 000
1991	39 300

Fig. 2. (*a*) Size structure of yellow eels resulting from sampling program in spring 1989 and in spring 1990. (*b*) Size structure of silver eels resulting from sampling the 1989 autumn catch and the 1990 autumn catch.

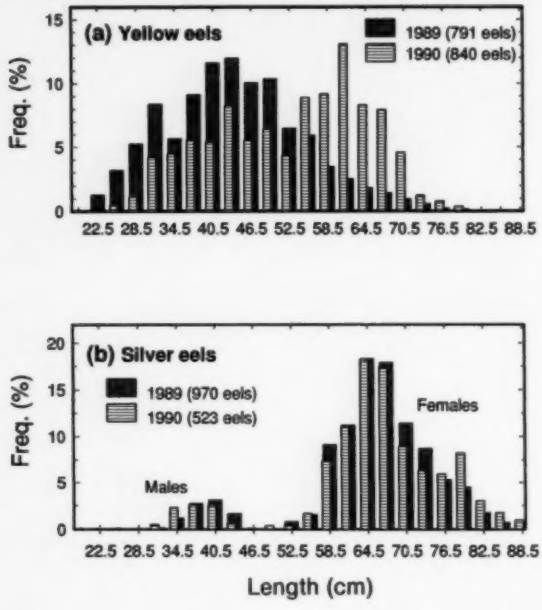
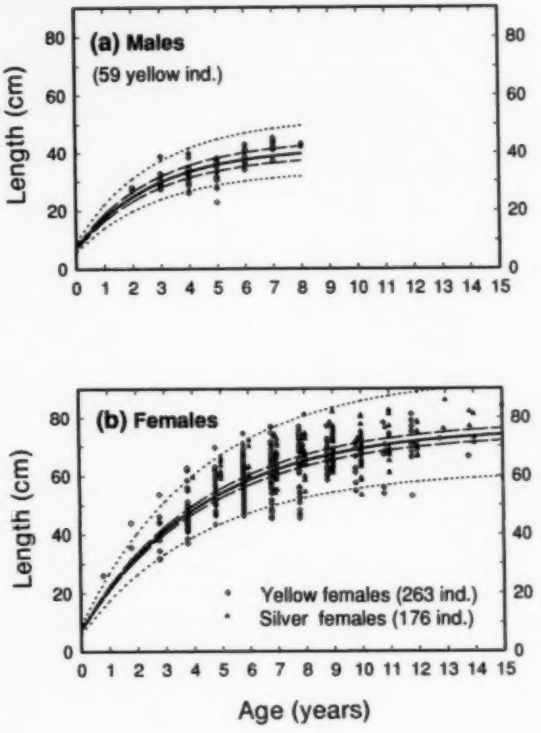


Fig. 3. Age (years) – length (cm) data for (*a*) 59 yellow males and (*b*) 439 females (263 yellow + 176 silver). Estimated Von Bertalanffy growth curves (thick line) are plotted along with the 95% confidence intervals (broken lines) and 95% prediction intervals (dotted lines). See Table 3 for regression statistics.


(a) Males
(59 yellow ind.)
Length (cm)
(b) Females
Length (cm)
Yellow females (263 ind.)
Silver females (176 ind.)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Age (years)

the female population seems to never reach sexual maturity. In fact, some old yellow specimens (>8–9 years) remain in the lagoons, as shown in several samples collected in 1976 (Rossi 1979; Gatto and Rossi 1979), in 1982–1984 (Rossi et al. 1987–1988), 1989, and 1990 (Carrieri et al. 1992). In contrast, all yellow males are likely to undergo metamorphosis within 4–7 years. (*v*) The age at metamorphosis is not fixed (Rossi and Colombo 1976*a*). With respect to the last point, it has been observed that slow-growing eels (both males and females) undergo metamorphosis at older ages, while fast-growing eels reach sexual maturity at younger ages. The emerging evidence (Vøllestad and Jonsson 1986; Vøllestad 1992) suggests that transformation from yellow to silver eels is largely dependent upon body size.

The model

The model derived here relies on the conceptual scheme in Fig. 4. It should be noted that the portion of the eel life cycle that is spent outside the lagoons, i.e., the larval and glass stages (Tesch, 1977), is disregarded, because the recruitment of elvers from the sea is independent of the local phenomena occurring in the lagoons. Attention is focused on population dynamics from the elver stage on.

Population variables

Let l be the size of newly recruited individuals (age x_0) in year t. We suppose it is a random variable with (known) probability density $r(l)$. From now on, size will be assumed to be length, although a variety of other size indicators such as weight could be used. Therefore, the integral:

$$\int_{l_1}^{l_2} r(l)\,dl$$

gives the probability of an elver being of a size between l_1 and l_2 ($l_1 < l_2$). If $R(t)$ is the overall number of newly recruited individuals in year t, the expected density $Y(x_0,l,t)$ with respect to l of elvers at time t is given by:

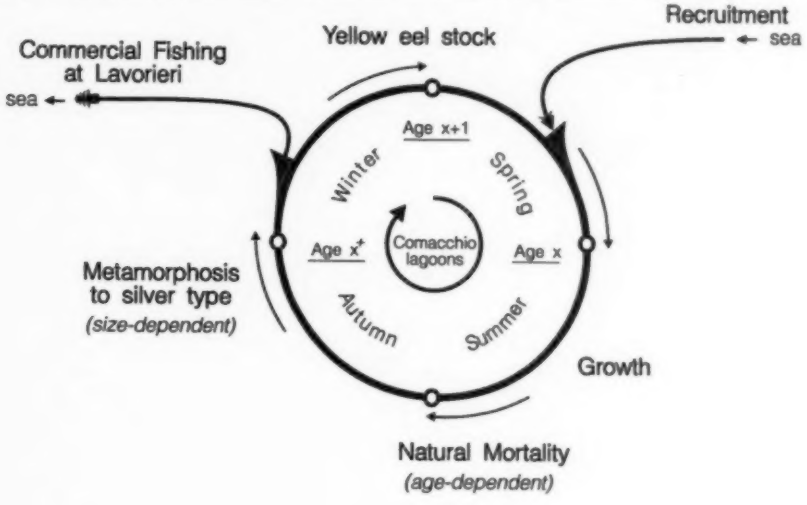
$$Y(x_0,l,t) = R(t)r(l)$$

The size structure of a cohort changes in time as a consequence of growth, survival, and maturation processes. The population variable $y(x,l,t)$ will be used to denote the joint probability density for a yellow eel to be of size l at age x and time t. Unlike r, y is a joint probability function, i.e., the probability that an elver, recruited in year $t - x$, remains in the yellow compartment x years after the transformation from the glass to elver stage and reaches length l. In fact, eels eventually leave the yellow compartment, because either they die (mainly as a consequence of anoxic conditions in summer) or they metamorphose to the silver stage (in autumn).

Table 2. The estimated length (cm) – weight (g) logarithmic relationship, obtained from 579 yellow eels and 669 silver eels, respectively.

	Equation	R^2	F	df	P
Yellow eels (males + females + elvers)	$\ln(w) = 3.37\ln(l) - 7.95$	0.97	21 475	577	<0.001
Silver eels (males + females)	$\ln(w) = 3.18\ln(l) - 7.07$	0.92	8 009	667	<0.001

Fig. 4. Schematic representation of the eel life cycle in the Comacchio lagoons.



The expected density $Y(x,l,t)$, with respect to l, of x-year-old yellow eels at time t is thus given by

$$Y(x,l,t) = R(t - x)y(x,l,t)$$

where $R(t - x)$ is the recruitment at time $t - x$. Therefore, if l_{max} is the maximum length and x_{max} the maximum age, then

$$[1] \qquad \Theta(x,t) = \int_0^{l_{max}} R(t-x)y(x,l,t)\,dl$$

represents the total number of yellows of age x at time t, while

$$[2] \qquad \Psi(t) = \sum_{x=x_0}^{x_{max}} \left[\int_0^{l_{max}} R(t-x)y(x,l,t)\,dl\right]$$

is the total number of yellow eels in the lagoons at time t.

The population variables $s(x,l,t)$ and $S(x,l,t)$ are defined for silver eels by analogy to $y(x,l,t)$ and $Y(x,l,t)$. A variety of parameters can be derived from these population variables. By using the weight–length relationship $w(l)$ (Table 2), it is possible to compute the total biomass of yellow eels at any given age x and time t

$$[3] \qquad \int_0^{l_{max}} w_Y(l)R(t-x)y(x,l,t)\,dl$$

and the overall biomass of silver eels (which coincides with the total catch in the Valli di Comacchio):

$$[4] \qquad \sum_{x=x_0}^{x_{max}} \left\{\int_0^{l_{max}} w_S(l)R(t-x)s(x,l,t)\,dl\right\}$$

The length structure of both yellow and silver eels can be easily derived from the length structures of the corresponding age-classes and, therefore, the frequency distribution of sizes in year t is simply given by

$$[5a] \qquad \pi_l^Y(t) = \frac{\sum_{x=0}^{x_{max}} Y(x,l,t)}{\int_0^{l_{max}} \left[\sum_{x=0}^{x_{max}} Y(x,l,t)\right] dl}$$

$$[5b] \qquad \pi_l^S(t) = \frac{\sum_{x=0}^{x_{max}} S(x,l,t)}{\int_0^{l_{max}} \left[\sum_{x=0}^{x_{max}} S(x,l,t)\right] dl}$$

Body growth

To describe age–length data, the Von Bertalanffy growth model has been chosen, among the models listed in Schnute (1981) and Seber and Wild (1989), because it seems to yield the best fit to our data. It is given by

$$[6] \qquad L(x) = L_\infty - (L_\infty - L_0)e^{-kx}$$

Table 3. Results of the age (years) – length (cm) nonlinear logarithmic regression (Von Bertalanffy growth model with a multiplicative error) performed on 59 males and 437 females.

	L_∞	k [years^{-1}]	$\sigma^2_{\ln(g)}$	R^2	df
Males	41.8±2.3	0.35±0.056	0.120	0.901	57
Females	76.2±1.4	0.23±0.010	0.116	0.938	435

Note: The equation was $\ln[L(x)] = \ln\{L_\infty (1 - e^{-kx}) + L_0 e^{-kx}\} + \ln(g)$.

where k [t^{-1}] is a measure of growth rate, L_∞ is the maximum reachable length and L_0 is the length of elvers at age 0. As a matter of fact, Eq. 6, being deterministic, is actually a poor descriptor of the age–length data, because eel growth rate is extremely variable among individuals (see Fig. 3). Therefore, some degree of variability should be added to Eq. 6. Kirkpatrick (1984) gives an extensive overview of stochastic body-size growth models. For our purposes it is sufficient to recall that the observed variability may be treated as the expression of genetic differences among individuals, and that these differences are already set at the metamorphosis from the glass to the elver stage (Kirkpatrick refers to this approach as the assignment at birth model). Growth trajectories of eels are, thus, completely determined for the rest of their life. Formally, the actual length $l(x)$ of an individual at age x can be computed:

$$[7] \qquad l(x) = L(x)g$$

where $L(x)$ is the expected length at age x given by Eq. 6 and g a growth factor randomly assigned to each eel according to some distribution function. A lognormal distribution of size of individuals within a cohort works well in most cases and is more appropriate than the normality assumption because the latter implies individuals with negative size (as suggested by Kirkpatrick (1984), it should be applied only when the length variance is small relative to the mean).

By definition, g has a unitary geometric mean, while its variance σ^2_g must be estimated from age–length data. If a logarithmic transformation of Eq. 7 is performed, one obtains

$$[8] \qquad \ln(l(x)) = \ln(L(x)) + \ln(g), \qquad \ln(g) \sim N(0,\sigma^2_{\ln(g)})$$

In our case, L_0 has been assumed to be 75 mm, following D'Ancona (1959, 1960) and Vøllestad and Jonsson (1986), while L_∞, k and $\sigma^2_{\ln(g)}$ have been evaluated by using a nonlinear least squares estimator (Table 3, Fig. 3) on the available data.

The stochastic growth model is related to the probability density $r(l)$ previously introduced. In fact, $r(l)$ is lognormally distributed with mean and variance given by

$$[9] \qquad E[r(l)] = L(x_0), \qquad \mathrm{Var}[r(l)] = [L(x_0)]^2 \cdot \sigma^2_g$$

Eel size within a cohort remains lognormally distributed, provided that no other size-dependent processes (such as those relative to sexual maturation) apply. An immediate derivation from Eqs. 6 and 7 shows that (Ricker 1975):

$$l(x + 1) = L_\infty(1 - e^{-k})\, g + l(x)\, e^{-k}$$

which is a two-parameter relationship between the length $l(x)$ and the subsequent length $l(x + 1)$ 1 year later. In eels growth occurs mostly during the warm summer months with winter growth being negligible. The size at the end of autumn (just before the fishing season) can be thus assumed approximately equal to eel size at the beginning of the following spring, i.e.:

$$[10] \qquad l(x^+) = l(x + 1)$$

Following Schnute's notation (1987) for the sake of simplicity, we replace $l(x)$ by l and $l(x + 1)$ by l^+. The growth model is then stated synthetically as

$$[11] \qquad l^+ = g\Lambda + \rho l; \qquad \Lambda \equiv L_\infty(1 - e^{-k}),\ \rho \equiv e^{-k}$$

Equation 11 is the keystone that will allow us to propagate in time the probability distribution function of eel size within a cohort, as will be shown in the next section.

Survivorship

Extreme anoxic conditions, which occur frequently in July and August, are the main cause of mortality (Rossi et al. 1987–1988). Conversely, most eels are likely to survive the winter season (unless water temperature falls below 0°C), as they can strongly reduce feeding activities and metabolic rate and enter a state of torpor (Nyman 1972; Sadler 1979; Walsh et al. 1983; Vøllestad 1986*b*). Therefore, natural mortality during the winter season is assumed to be negligible.

Summer mortality, on the contrary, cannot be neglected. In the most general case, summer mortality may be conceived of as a function of both size and age. Let $\sigma(x,l)$ be the survival from age x to age x^+ and from size l to size l^+, i.e., the fraction of individuals of age x and size l able to survive from the beginning of spring to the end of summer. We have above defined

$$\int_{l_1}^{l_2} y(x,l,t)\, dl$$

as the probability that an x-year old yellow eel is between l_1 and l_2 ($l_1 < l_2$) at time t. The same probability at the end of the warm season (age x^+ and time t^+) can be computed as follows:

$$[12] \qquad \int_{l_1^+}^{l_2^+} y(x^+,l,t^+)\, dl = \int_{l_1}^{l_2} \sigma(x,l) y(x,l,t)\, dl$$

where:

$$[13a] \qquad l_1^+ = g_1\Lambda + \rho l_1 \qquad l_2^+ = g_2\Lambda + \rho l_2$$

$$[13b] \qquad g_1 = \frac{l_1}{L(x)} \qquad g_2 = \frac{l_2}{L(x)}, \qquad l_1 < l_2$$

Note that Eqs. 12 and 13 explicitly imply that eel length scatters on wider and wider intervals (Fig. 5), because the size-class (l_1, l_2) is always smaller than (or at most equal to) its projection (l_1^+, l_2^+) 6 months later.

It should be noted that, if no yellow eel of size l underwent metamorphosis during autumn, the joint distribution of age and size at the beginning of the following spring season would simply equal the distribution 6 months earlier:

$$[14] \qquad y(x+1, l^+, t+1) = y(x^+, l^+, t^+)$$

because winter growth is assumed to be negligible (Eq. 10). Equations 12–14 allow the temporal propagation of the probability distribution of eel lengths provided there is no metamorphosis.

Whether natural mortality is actually dependent upon eel age or size, or both size and age, is difficult to say. Available data do not shed light on this problem, and no suitable field experiment has been ever done to clarify this point. Because of the lack of information, we will assume an age-dependent survivorship. In particular, age at death is assumed to have a Weibull distribution (Johnson and Kotz 1970; Pinder et al. 1978):

$$Q(x) = 1 - \exp[-((x - x_0)/b)^c], \qquad b, c > 0$$

where $Q(x)$ gives the probability of dying before age x and b and c are the scale and shape parameters, respectively, of the Weibull distribution.

Therefore, age-specific survivorship in the interval between x and x^+ can be easily computed as

$$[15] \qquad \sigma(x) = \exp\left(\left(\frac{x - x_0}{b}\right)^c - \left(\frac{x - x_0 + 1}{b}\right)^c\right)$$

The Weibull distribution is rather flexible and can possess either positive or negative skewness. It can be shown (Pinder et al. 1978) that (*i*) $\sigma(x)$ is a decreasing function of age when $c > 1$; (*ii*) $\sigma(x)$ is constant when $c = 1$; and (*iii*) $\sigma(x)$ is an increasing function of age when $c < 1$. These patterns correspond respectively to type I, II, and III survivorship curves (Pearl 1928; Deevey 1947).

Sexual maturity

As already mentioned, the age at metamorphosis is not fixed, with males and females maturing to the silver stage at older ages growing more slowly than those maturing at younger ages (Vøllestad and Jonsson 1986; Vøllestad 1989). On this basis, we will assume that the metamorphosis rate is mostly dependent upon size, and not age. Let $\gamma(l)$ be the expected fraction of yellow eels of size l that undergo metamorphosis to the silver stage in autumn. Then, the probability density function $s(x^+,l,t^+)$ that an elver, recruited in year $t - x$, becomes an x^+-year-old silver eel of size l can be easily derived from $y(x^+,l,t^+)$:

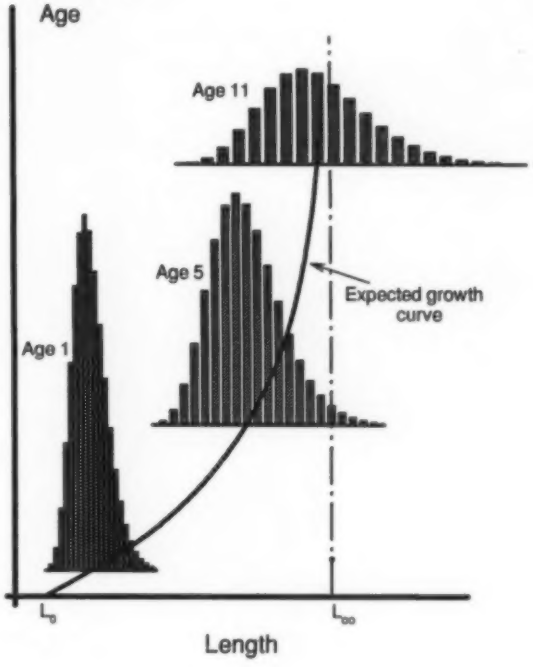
$$[16] \qquad s(x^+,l,t^+) = \gamma(l)\, y(x^+,l,t^+)$$

On the other hand, the probability density of retention in the lagoons as yellow type at the end of the fishing season is

$$[17] \qquad y(x+1,l,t+1) = [1 - \gamma(l)]\, y(x^+,l,t^+)$$

This equation replaces eq. (14) of the previous section where metamorphosis was not accounted for. As sexual maturation is assumed to be size dependent, the probability distribution function of yellow eel size will be altered by this process as soon as yellow eels become large enough to metamorphose to silver type; therefore in the general case, size structure within a cohort will no longer be lognormal.

Fig. 5. The evolution of eel size structure within a cohort. L_0 and L_∞ are parameters of the Von Bertalanffy growth curve. The inclusion of a lognormally distributed growth factor determines the dispersion of eel sizes on wider and wider intervals.



Because bigger eels are more likely to undergo metamorphosis than the smaller ones, $\gamma(l)$ must be an increasing function of l. Based on the shape of the ascending limb of silver male and female size distributions (see Fig. 2), we have here assumed a sigmoidal metamorphosis function defined by:

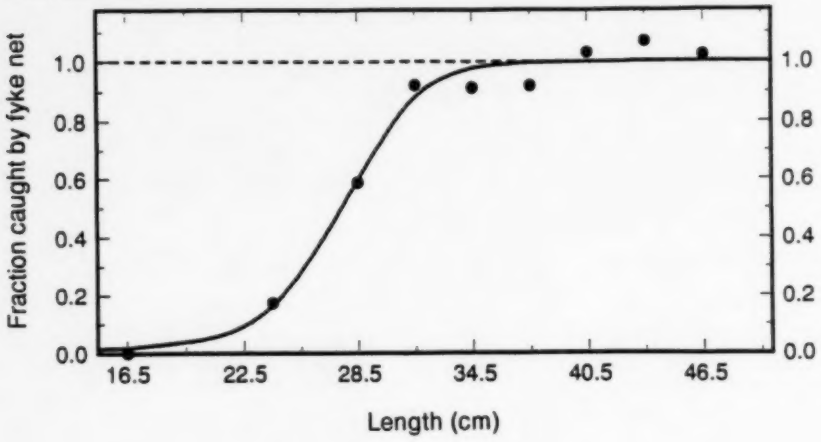
$$[18] \qquad \gamma(l) = \frac{\gamma \max}{1 + \exp\left(\dfrac{l - \lambda}{\eta}\right)}, \qquad \gamma_{max}, \lambda, \eta > 0$$

where γ_{max} (≤ 1) is the maximum rate of metamorphosis, λ is a semisaturation constant, and η is a parameter inversely proportional to the slope of the metamorphosis curve at $l = \lambda$. When λ and η are positive, $\gamma(l)$ increases with eel size and levels off to γ_{max} for large values of l.

Net selectivity

The fishing device used to sample yellow eels (fyke net with an 8-mm mesh) is size selective: only larger animals are caught, and most elvers are able to escape through the meshes of the net. Therefore, the length structure derived from 1989 and 1990 data is not the size distribution

Fig. 6. Fyke net selectivity curve (8-mm mesh size) as resulting from a mark–recapture experiment performed in the Comacchio lagoons in 1982 (Rossi et al. 1987–1988). The black dots are the normalized ratios between recaptured and marked eels in each (3-cm-wide) size-class.



π_l^Y computed from $Y(x,l,t)$ (Eq. 5), as the latter refers to all fish living in the lagoons, while the former concerns only the eels captured by fishing gear. A corrected yellow eel size distribution is to be derived to take into account fish liability to capture as a function of size. To this end, we have assumed that the fraction Φ of eels caught in the net is a function of the eel cross section A according to the following equation:

$$[19] \qquad \Phi(A) = \frac{1}{1+\exp\left(\dfrac{A_{med}-A}{\zeta}\right)}, \qquad A_{med}, \zeta > 0$$

where ζ (slope of selectivity function) and A_{med} (median cross section) are to be estimated. As our demographic model uses length classes, we need to derive the eel section A as a function of l. To this purpose, note that the weight w (grams) is given by

$$[20] \qquad w = \delta A l$$

where δ is the specific weight of eels, assumed to be a constant. The weight–length relationship (Table 2) is

$$[21] \qquad w(l) = \alpha l^{\beta}$$

Matching Eq. 20 with Eq. 21 yields

$$[22] \qquad A = \alpha/\delta \; l^{\beta-1}$$

and Eq. 19 can be rewritten as:

$$[23] \qquad \Phi(l) = \frac{1}{1+\exp\left(\dfrac{A_{med}-(\alpha/\delta)l^{\beta-1}}{\zeta}\right)}$$

The value of ζ and A_{med} of Eq. 23 have been estimated from the data of a mark–recapture experiment performed with the same fishing device by Rossi et al. (1987–1988) in the Comacchio lagoons in 1982. The estimated selection curve is shown in Fig. 6.

Therefore, the expected size distribution of yellow eels captured in fyke nets can be computed from the density $Y(x,l,t)$:

$$\pi_l^{Y^*}(t) = \frac{\sum_{x=0}^{x_{max}} \Phi(l) Y(x,l,t)}{\int_0^{l_{max}} \left[\sum_{x=0}^{x_{max}} \Phi(l) Y(x,l,t)\right] dl}$$

Further considerations

Sexual dimorphism

Because of sexual dimorphism, females and males must be represented by different state variables, that is, $y^F(x,l,t)$, $y^M(x,l,t)$, $s^F(x,l,t)$ and $s^M(x,l,t)$ for yellow females, yellow males, silver females and silver males, respectively. Therefore, length and age structure will be different in the two sexes. Females and males share the same survivorship function $\sigma(x)$, while the metamorphosis function $\gamma(l)$ and the expected growth curve $L(x)$ differ in the two sexes. Maximum metamorphosis rate from yellow to silver male has been set equal to 1, because all surviving males eventually reach sexual maturity (Gatto and Rossi 1979).

Time invariance of model parameters

We make the strong assumption that growth, survivorship, and metamorphosis parameters are constant over time. However, the emerging evidence in field ecology is that time invariance is an exception rather than a rule. Actually, we tend to believe that at least recruitment abundance (which we treat as an exogenous parameter, because it is independent of eel abundance in the lagoons) may be variable from year to year (Vøllestad 1986*b*; Vøllestad and Jonsson 1988). On the other hand, to reconstruct the time series of recruitments is beyond hope, because we lack suitable historical series of length distributions of yellow

and silver eels. Also, the commercial catch, after the dramatic drop at the end of the 1970s, has fluctuated in the last decade (Table 1) around a mean value of about 6.15 kg/ha with a standard deviation of 1.66, which is large but not enormous. Within this context, the unavoidable assumption is that recruitment is distributed around a constant average value $R(t) = \varepsilon_t R_a$, where ε_t is a random factor with unitary geometric mean. R_a is the parameter we will try to estimate under the further hypothesis that the variance of ε_t is not too large. In fact, if this is the case and no disturbance factors have been acting on the population for a number of years, stable age (and stable size) distributions are reached. In other words, population variables may be considered to be substantially stationary, namely

$$y(x,l,t+1) = y(x,l,t) = y(x,l) \text{ and } s(x,l,t+1) = s(x,l,t) = s(x,l).$$

In practice, there will be variations from year to year, but these should be small provided the variance of ε_t (and of the other parameters) is small. The size structure of both females and males (π_l^Y, $\pi_l^{Y^*}$ and π_l^S) depends upon all model parameters except R_a. In fact, it is easy to prove that

$$[24a] \quad \pi_l^Y = \frac{\sum_x Y(x,l)}{\int \sum_x Y(x,l)\,dl} = \frac{\sum_x y(x,l)}{\int \sum_x y(x,l)\,dl}$$

$$[24b] \quad \pi_l^{Y^*} = \frac{\sum_x \Phi(l) Y(x,l)}{\int \sum_x \Phi(l) Y(x,l)\,dl} = \frac{\sum_x \Phi(l) y(x,l)}{\int \sum_x \Phi(l) y(x,l)\,dl}$$

$$[24c] \quad \pi_l^S = \frac{\sum_x S(x,l)}{\int \sum_x S(x,l)\,dl} = \frac{\sum_x s(x,l)}{\int \sum_x s(x,l)\,dl}$$

where $y(x,l)$ and $s(x,l)$ are computed recursively using Eqs. 9, 12, 13, and 15–18. Consequently, size structure of yellow and silver eels is determined only by the elvers' length distribution $r(l)$ at recruitment (not by the corresponding abundance) and by growth, death, and sexual maturation processes, which have been assumed to be time independent.

Model calibration and validation

A direct comparison of the 1989 and 1990 size distributions (Fig. 2) points out that the histograms of silver eels are quite similar (Kolmogorov–Smirnov test, $D = 0.071$, $p > 0.05$), while those of yellow eels are different (K.S. test, $D = 0.3723$, $p < 0.001$). In particular, the 1990 yellow distribution is skewed in favor of small sizes. The reason for this phenomenon is that during 1989 a considerable number of juvenile yellows (1–3 years old) were stocked into the lagoons in the period following the sampling program. As only a negligible fraction of yellows reach sexual maturity at the typical sizes attained at ages 1^+, 2^+, and 3^+, we can assume that the 1989 size distributions of both silver and yellow eels were not affected by restocking. Therefore, we have proceeded in the following way: the 1989 yellow and silver distributions have been considered stable distributions (see previous section) and have been used to estimate model parameters; the 1990 data, supplemented with information on restocking, have been used for validating the demographic model.

Unknown parameters

For females, three coefficients, λ^F_{max}, λ^F, and η^F, of the metamorphosis function are to be estimated, whereas for males λ^M and η^M only, because γ^M_{max} equals unity. The survivorship curve has two unknown parameters, b and c. The age x_0 at which eels are recruited to the fishery is set to 1 year while the corresponding abundance R_a must be estimated. Altogether, model calibration requires that eight unknown parameters be estimated.

Estimation of unknown parameters

To estimate unknown parameters, the expected length distributions and the expected commercial catch have been compared, respectively, with the observed length distributions of 1989 and the mean yield between 1977 and 1991 (ca. 6.15 kg/ha). As length distributions do not depend on recruitment abundance under the time-invariance assumption, we have first derived the estimates of all parameters except R_a by minimizing the following objective function:

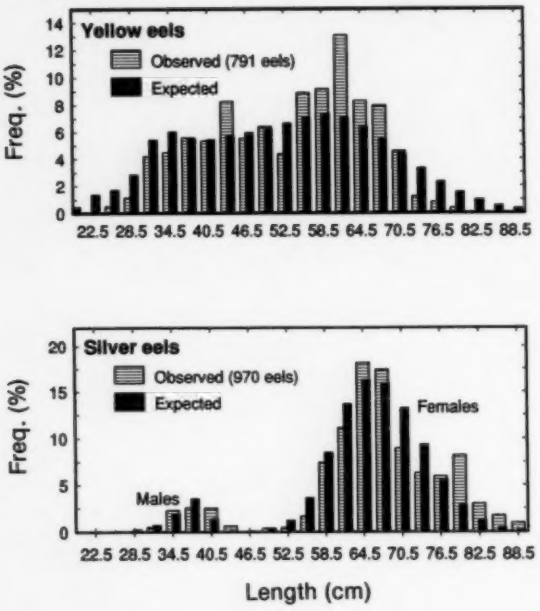
$$[25] \quad \Xi(\gamma^F_{max}, \lambda^F, \eta^F, \lambda^M, \eta^M, b, c) = \int (\bar{\pi}^{Y^*} - \hat{\pi}^{Y^*})^n\,dl + \int (\bar{\pi}^S - \hat{\pi}^S)^n\,dl$$

where $\bar{\pi}^{Y^*}$ and $\bar{\pi}^S$ are the observed size structures of yellow and silver eels, $\hat{\pi}^{Y^*}$ and $\hat{\pi}^S$ are the expected counterparts computed by means of Eq.s 24*b* and 24*c*, and n is an even and positive integer. Equations 12, 13, and 15–18 are recursively used to simulate the life cycle of a cohort; in practice, the probability density function $r(l)$ of recruited individuals, estimated from age–length data according to Eqs. 8 and 9, is propagated through ages. Each simulation is run with a different set of values for the seven parameters to be estimated until the best fit to the observed size distribution is obtained. A downhill simplex method (Press et al. 1988) has been applied to find the parameter values that minimize Ξ. An n of 4 is a fair compromise between convergence speed and goodness of fit to size-distribution tails.

Once the optimal value of the first seven parameters has been obtained, the recruitment estimate can be easily computed if one considers that commercial catch is a linear function of R_a under the time-invariance assumption:

$$[26] \quad \hat{\text{Catch}}(R_a/\hat{\gamma}^F_{max}, \hat{\lambda}^F, \hat{\eta}^F, \hat{\lambda}^M, \hat{\eta}^M, \hat{b}, \hat{c}) = \sum_{x=x_0}^{x_{max}} \left\{ \int_0^{l_{max}} \bar{w}_S(l)[R_a \hat{s}(x,l)]\,dl \right\} = \left\{ \sum_{x=x_0}^{x_{max}} \left[\int_0^{l_{max}} \bar{w}_S(l) \hat{s}(x,l)\,dl \right] \right\} R_a$$

Fig. 7. Observed versus expected size distributions for 1989. The expected values are computed via the best fitting model.



Therefore, given the value of $\hat{\gamma}^{F}_{max}$, $\hat{\lambda}^{F}$, $\hat{\eta}^{F}$, $\hat{\lambda}^{M}$, $\hat{\eta}^{M}$, $\hat{b}$, and $\hat{c}$, one can compute the recruitment abundance that provides the mean observed catch (6.15 kg/ha):

$$[27] \qquad \hat{R}_a = \frac{6.15}{\sum_{x=x_0}^{x_{max}} \left[\int_0^{l_{max}} \overline{w}_S(l)\hat{s}(x,l)\,dl \right]}$$

Parameter uncertainty estimation

To evaluate the variance of parameter estimates, nonparametric statistics have been used. Bootstrapping is undoubtedly one of the most widespread computing-intensive techniques recently applied in ecological studies (for an extensive review of methods based on resampling plans see Efron 1982). In the bootstrap procedure, original data are randomly recombined B times (replicates), pseudovalues of unknown parameters are computed for each recombination of the original data and the statistics of the parameters of interest are derived from the resulting frequency distributions.

In this study, we basically use bootstrapping procedures with the aim of reproducing sampling variability from the whole population in the lagoons. The simplest way of generating a bootstrap replicate would be to place the original data set of m eels (m = 970 for silver eels, m = 791 for yellows) into a pool and randomly extract m animals with replacement. Replacement means that each sampled eel is to be reinserted into the pool before another eel is sampled: thus, any eel of the original data set may be represented more than once in a bootstrap replicate or may not be present at all. This simple resampling scheme assumes an equal probability of selection of every fish in the catch. This is not true for stratified samples (Efron and Tibshirani 1986), because eels sampled in different strata, fishing periods, and lagoons do not share the same probability of being drawn from the pool. To be consistent with the original sampling design described in the second section, the process of bootstrap replication requires that any eel is drawn with a probability reflecting its subsample and stratum abundances, the different fishing periods, and the catch in the three lagoons. The procedure implemented to accomplish this resampling scheme is described in detail by Pelletier and Gros (1991).

Despite its reputed superiority when compared with other resampling techniques such as jackknifing (Efron 1982), bootstrapping has been applied rarely to parameter estimation in fish dynamics, primarily because it can be tremendously time consuming. The precision of a bootstrap estimate, in fact, strictly depends on how many times the original data are randomly recombined (i.e., how many replicates, B, are performed within a bootstrap calculation). Bootstrap estimates will converge to a stable value as B becomes large, by the law of large numbers. To have a stable bootstrap estimator, we recombined the data 1000 times (B = 1000). About 8 h of computing time on a Workstation HP-720 were necessary to complete the bootstrap calculation. We define $\theta^{*}_{i,j}$ as the value of the jth parameter (j = 1 2, ..., 8) estimated from the ith bootstrap replicate (i = 1, 2, ..., 1000). The mean value θ^{B}_{j} and the variance of the B pseudo values $\theta^{*}_{i,j}$ are

$$\theta^{B}_{j} = \frac{1}{B}\sum_{i=1}^{B}\theta^{*}_{i,j}$$

$$\mathrm{Var}(\theta^{B}_{j}) = \frac{1}{B}\sum_{i=1}^{B}(\theta^{*}_{i,j} - \theta^{B}_{j})^2$$

Let θ^{true}_{j} be the true value of θ_j. As Meyer et al. (1986) state, if the full sample estimator for the original data set, θ^{all}_{j}, is a biased estimate of θ^{true}_{j}, then θ^{B}_{j} will equally be biased, because it estimates θ^{all}_{j}, rather than θ^{true}_{j}. Therefore, a bias-adjusted bootstrap estimate of θ^{true}_{j} is $\theta^{B-adj}_{j} = \theta^{all}_{j} - \theta^{B}_{j}$ (see Meyer et al. (1986) for details) A number of statistics (median, mode, skewness, etc.) were then computed from the frequency distributions of the 1000 values ($\theta^{*}_{1,j}$, $\theta^{*}_{2,j}$, ..., $\theta^{*}_{1000,j}$, j = 1, 2, ..., 8). Furthermore, a bias-corrected percentile method has been adopted (Efron 1982) to derive the interval between the 5th and 95th percentile values as a candidate for a 90% confidence interval of each parameter.

Model validation

The model has been validated against the data collected in 1990. As anticipated, the 1990 size distributions are influenced by the restocking carried out the year before. According to Carrieri et al. (1992), 35.9 t of elvers were stocked in the lagoons between April and May 1989, soon after the yellow eel sampling described in the second section. The average body weight was 20 ± 7.8 g, with 30% of the specimens being 1 year old, 40% being 2 years old, and 30% being 3 years old. The validation procedure is

Table 4. Main statistics (bias adjusted expected value, SD, bias corrected 5th and 95th percentile, and standardized skewness) obtained from the frequency distributions of the 1000 bootstrap estimates.

Parameters	Expected value	SD	Percentile 5th	Percentile 95th	Standardized skewness
b	0.98	0.54	0.17	1.97	3.77
c	0.30	0.07	0.18	0.43	2.07
γ^{F}_{max}	0.12	0.03	0.07	0.17	10.52
λ^{F}	58.40	0.76	57.30	59.70	11.17
λ^{M}	39.10	1.63	36.80	42.10	−7.69
η^{F}	2.40	0.50	1.75	3.25	22.08
η^{M}	2.80	0.52	1.99	3.69	22.89
R_a	136.80	66.64	70.00	267.78	25.00

Table 5. Correlation matrix of the eight estimates. The significance level corresponding to each correlation coefficient is reported in brackets.

	b	c	γ^{F}_{max}	λ^{F}	λ^{M}	η^{F}	η^{M}	R_a
b								
c	0.552							
	(0)							
γ^{F}_{max}	0.029	−0.450						
	(0.355)	(0)						
λ^{F}	0.046	0.090	0.589					
	(0.146)	(0.004)	(0)					
λ^{M}	0.015	0.634	−0.656	−0.131				
	(0.636)	(0)	(0)	(0)				
η^{F}	0.054	−0.129	0.496	0.559	−0.257			
	(0.087)	(0)	(0)	(0)	(0)			
η^{M}	−0.035	0.160	−0.135	0.034	0.419	−0.126		
	(0.274)	(0)	(0)	(0.284)	(0)	(0)		
R_a	−0.438	0.313	0.622	−0.098	0.590	−0.186	0.174	
	(0)	(0)	(0)	(0.002)	(0)	(0)	(0)	

as follows. First, estimates $\hat{Y}(x^{+},l,1989^{+})$ of yellow eel abundances in autumn 1989 are obtained by using the model fitted to the 1989 data. By applying Eq. 17 to $\hat{Y}(x^{+},l,1989^{+})$ one can then derive the expected distribution and abundance of naturally recruited yellow eels at the beginning of spring 1990. However, this is not sufficient to obtain $\hat{Y}(x^{+},l,1990)$, because the contribution resulting from elver stocking must be accounted for. This contribution can be calculated by using Eqs. 12, 13, and 17 and the estimated vital rates to propagate through time the size distributions and abundances of the three restocked cohorts. In fact, a mark–recapture study conducted by Rossi et al. (1988) indicated that restocked eels adapt to the new environment and exhibit growth, survival, and metamorphosis rates that resemble those of naturally recruited eels. The length distributions resulting from the three cohorts are combined with the size distribution resulting from the natural recruitment, according to the respective abundances in each size-class, to yield $\hat{Y}(x^{+},l,1990)$. The final expected distribution of yellows in the spring of 1990 is obtained by applying net selectivity (Eq. 23) and normalizing. It is then compared with the sample distribution in spring 1990 to assess on the validation quality. Finally, Eqs. 12, 13, and 16 are applied to $\hat{Y}(x^{+},l,1990)$ to forecast the expected silver eel distribution, which is compared with the observed size structure of the 1990 silver eel catch for further validation.

Results

Expected versus observed size distributions of yellow and silver eels in 1989 are plotted in Fig. 7. The model fits the reference samples quite well, especially the silver distribution. Table 4 reports the bias-adjusted expected values of model parameters along with standard deviations, the bias-corrected 5th and 95th percentile and the standardized skewness, as defined in the previous section. The estimates of λ^{F}_{max}, λ^{F}, η^{F}, λ^{M}, η^{M}, and c can be considered good, because all these parameters have standard deviations of less than 25% of the corresponding average. The expected values of b and R_a are less accurate, a likely consequence of the negligible proportion of elvers in the

Fig. 8. Frequency distribution of eel recruitment (kg/ha) resulting from the 1000 pseudovalues obtained by bootstrapping. Expected recruitment is about 1.2 kg/ha.

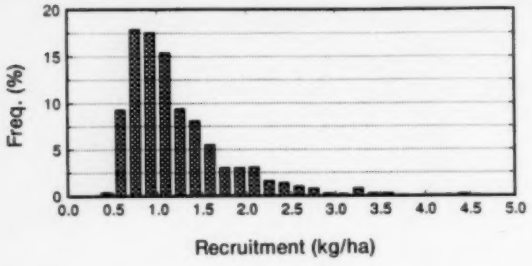
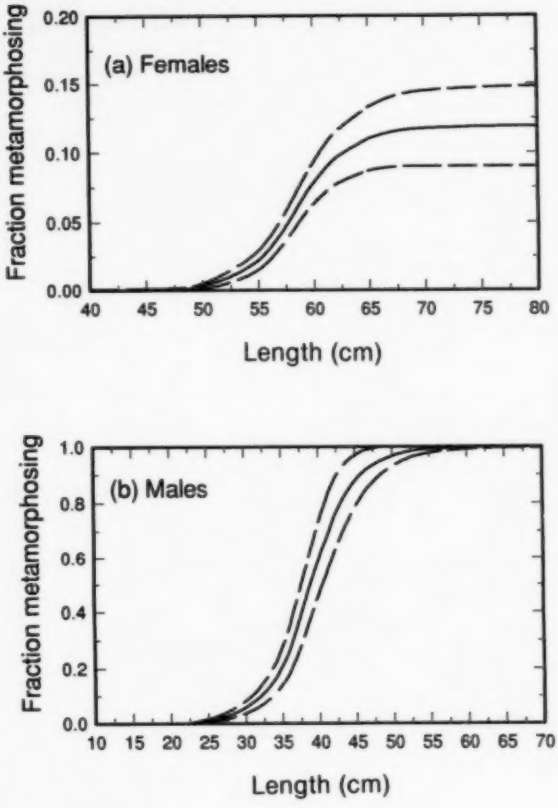


Fig. 9. Expected metamorphosis curve (±SD) for (*a*) females and (*b*) males.



yellow sample. The correlation matrix computed from the 1000 bootstrap replicates emphasizes moderate cross dependencies between model parameters (Table 5). The negative correlation (−0.438) between R_a and the scale factor b of the Weibull survivorship curve can be easily explained if one considers that b is positively correlated with survival: small increments of survival, corresponding to larger values of b, imply a larger fraction of eels reaching older stages. Therefore, the estimate of recruitment, computed by means of Eqs. 26 and 27, necessarily decreases so that the same catch of silver eels (6.15 kg/ha) is obtained. A similar remark also applies to the negative correlation (−0.622) between the recruitment and λ^F_{max}, the maximum fraction of yellow eels undergoing metamorphosis: again, if the rate of eels moving from the yellow to the silver compartment increases, R_a must decrease to match the yield of 6.15 kg/ha.

The knowledge of the distribution of the eight basic parameter estimates is rather arid information, but makes it possible to derive the main statistics of a number of important indices and vital rates that are of more immediate understanding and practical use. First, one can obtain recruitment in terms of biomass (per hectare), namely:

$$[28] \qquad R_w = \int w_Y(l)[Rr(l)]\, dl$$

which is a more meaningful figure than abundance. The bootstrap distribution of R_w (Fig. 8) has a rather large variance. In fact, it is made up of two components: one reflects the uncertainty in parameter estimation, and the other is related to the natural variance of recruitment (the variance of the noise factor ε_t). It should be noted that recruitment biomass, though fairly uncertain (1.2 ± 0.6 kg/ha; Fig. 8), is one order of magnitude smaller than the estimate obtained by Gatto and Rossi (1979) from the 1974–1976 data collected in the same lagoons (20 kg/ha). This difference actually corresponds to the dramatic drop in commercial catch that occurred at the end of the 1970s as a result of mismanagement of the fishery.

A second piece of information that can be derived from model calibration is the metamorphosis rate at each length. The average metamorphosis curve for females with the bootstrap standard deviation at each size is shown in Fig. 9*a*. The fraction of eels that reach sexual maturation is virtually negligible for sizes smaller than 55 cm, then it increases and levels off to 0.12 (γ^F_{max}) for sizes over 65 cm. In the case of males (Fig. 9*b*), saturation of the metamorphosis curve is reached for smaller lengths (50 cm). The accuracy of estimation, in terms of percent error with respect to the average metamorphosis rate is different at different body sizes. Note that the estimate of $\gamma^F(l)$ (Fig. 9*a*) is most accurate for central size-classes (about 60 cm), i.e., in the range comprising the largest fraction of silver eels. In any case, the percent error does not exceed 25% even for larger size-classes.

The other vital rate that follows easily from model calibration is survival at different ages (Fig. 10). Survivorship in the juvenile stage (35% from age 1 to age 2) is much smaller than that in the older age-classes for which it is roughly 90%. Estimates are quite accurate for these age groups, as demonstrated by the small standard deviations. Survival estimates are in agreement with those obtained by Gatto and Rossi (1979) ($\sigma_{x=1,2}$ = 38%, $\sigma_{x>2}$ = 80%) for the 1974–1976 data. A direct comparison with the Vøllestad and Jonsson (1988) estimates for the Imsa River (Norway) is not feasible, as their model is based on age-independent mortality.

Finally, we have evaluated the absolute density (both in terms of abundance per hectare and biomass per hectare) of yellow eels, information of particular interest, because it cannot be measured directly. Abundance of yellow eels is estimated as being 336 individuals per hectare, with

females comprising over 97% of the population. Silver eel abundance (12.1 individuals/ha) is only 3% that of yellows. Yet, the mean weight of silver eels (512 g) is larger than the yellows (188 g), because only the larger animals metamorphose. Therefore, the biomass of silver eels (6.15 kg/ha) is about 10% that of yellow eels (62.38 kg/ha). Further details regarding biomass are reported in Table 6 where we compare the absolute density (kilograms per hectare) of yellow and silver eels per size (Table 6*a*) and age group (Table 6*b*). The results can be summarized as follows. The first size (<30 cm) and age group (1–2 years) refer to the prereproductive stage (when no yellow eel undergoes metamorphosis to the silver stage) and comprise less than 5% of the eel biomass. The second and third size groups correspond, respectively, to silver males (30–45 cm) and silver females (>45 cm), because mature males are always smaller than adult females. It is worthwhile to note that both the sexual dimorphism and the allometric relation between size and weight contribute to skew the biomass distribution toward the larger size groups, with eels over 45 cm comprising roughly 90% of the biomass in the yellow stage. The age group from 3 to 7 year olds in Table 6*b* includes all the silver males, though a consistent fraction of yellow females undergoes metamorphosis from age 5^+ on. Therefore, the age structure of silver females overlaps that of silver males such that biomass distributions cannot be completely separated according to this classification. The older age group (>8 years), that consists of only females in both the silver and yellow stages, comprises more than 53% of the total biomass.

The results of model validation are displayed in Fig. 11. As stated before, in deriving the expected size distribution of yellow and silver eels in 1990, we have accounted for the contribution of elvers stocked at the end of April 1989. The model supplemented with the information on restocking fits the reference sample well. As a matter of fact, the introduction of the three cohorts largely affects yellow eel size structure in 1990, skewing the distribution towards the smaller size-classes. On the contrary, 18 months after restocking, the effects on the commercial catch are still hardly detectable, because only a small fraction of the eels introduced in 1989 attain the minimum length required to reach sexual maturation. Only the male distribution seems to be slightly affected, as males undergo metamorphosis at considerably smaller sizes than females.

Discussion

We have derived an age- and size-structured model that mimics the life cycle of eel populations with reasonable detail. Simpler models based on age-classes according to classical demographic theory are unrealistic for eels, because the transformation from yellow to silver stage appears to be largely dependent upon size rather than age, whilst the dispersion of animals of the same age on wide size intervals makes age a very poor indicator of eel length. Our approach is somewhat different from that of Kirkpatrick (1984), Schnute (1987), and Deriso and Parma (1988). In fact, they provide a complete theoretical framework for constructing and analyzing size-dependent models in which the resulting equations are analytically tractable in a closed

Fig. 10. Expected annual survival (± SD) as a function of age.

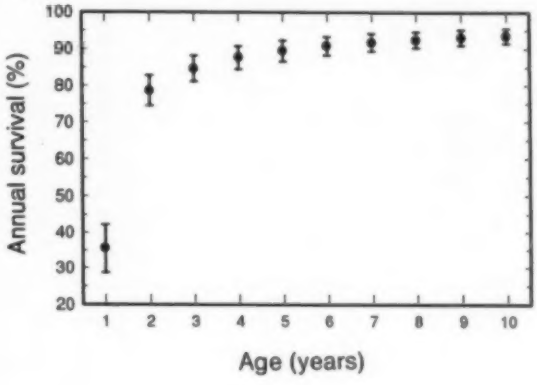
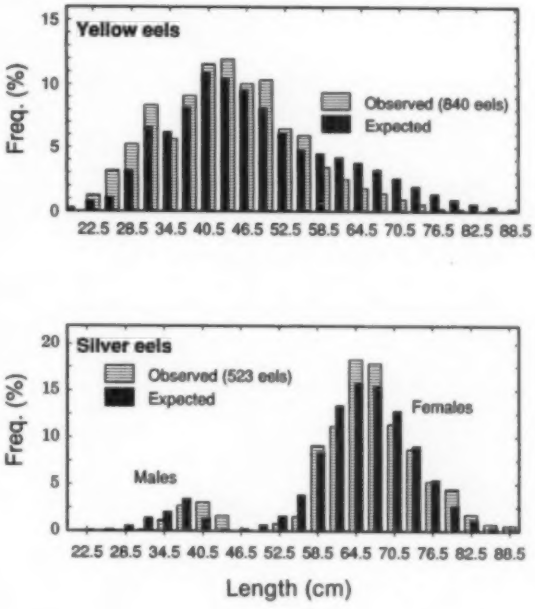


Fig. 11. Observed versus expected size distributions for 1990 (results of validation procedure). Expected distributions for yellow and silver eels are computed by explicitly accounting for elver restocking in April–May 1989, as detailed in the text.



form. The drawback of their approach is that this tractability is achieved by means of some strong hypotheses about the shape of the net-selectivity curves, the analytical expression of the mortality function and the structure of the stochastic growth model. In our work we fully retain Deriso and Parma's suggestion to "let the computer add the numbers" (Deriso and Parma 1988, p. 1055). Using a few realistic assumptions concerning net selectivity, growth, survival, and sexual maturation, we are able to numerically propagate through time the distribution function of eel sizes by

Table 6. 1989 absolute density (kg/ha) of yellow and silver eels, according to sex and to size and age groups.

(A) Densities by length classes.

Length (cm)	Yellow (spring)		Silver (autumn)		Yellow	Silver
	Males	Females	Males	Females	Male + female	Male + female
<30	0.09	1.35			1.44	
30–45	0.12	4.68	0.08		4.80	0.08
>45		56.14		6.07	56.14	6.07
Total	0.21	62.17	0.08	6.07	62.38	6.15

(B) Densities by age.

Age (years)	Yellow (spring)		Silver (autumn)		Yellow	Silver
	Males	Females	Males	Females	Male + female	Male + female
1–2	0.06	3.00			3.06	
3–7	0.15	25.63	0.08	2.19	25.78	2.27
≥8		33.55		3.88	33.55	3.88
Total	0.21	62.17	0.08	6.07	62.38	6.15

Note: Figures for yellows refer to spring (age x), those for silver eels to autumn–winter (age x^+).

recursive equations that update the distribution of lengths in any age class.

The model has been applied to the eel fishery of the Valli di Comacchio lagoons. Estimation of model parameters from 1989 data has led to the evaluation of natural survivorship, the rate of metamorphosis from yellow to silver type, and absolute abundance and biomass in each age- and size-class of each sex, for both yellow and silver eels. A similar assessment was previously carried out by Gatto and Rossi (1979) for the same fishery on the basis of the 1974–1976 catch data, by Vøllestad (1986*a*) for Hallangspollen Bight (Norway) and by Vøllestad and Jonsson (1988) for the Imsa River fishery (Norway). However, these authors used classical age-class models and did not provide validation, as we do here by using the 1990 data. Parameter uncertainty has been estimated via bootstrapping. It is worth noting that this statistical procedure (or similar resampling plans), although time-consuming, is to be recommended whenever nonanalytic models or analytic models of even moderate complexity are used. In fact, in these cases finding analytical properties of the estimators used to fit the data is beyond hope.

The weakest assumption of the present application is perhaps the time invariance of natural recruitment abundance. Unfortunately, the influence of the environment on recruitment and the effects of varying recruitment on population dynamics are scarcely documented for eel populations. Therefore, we had to exploit the available data, using only 1 year for calibration and one for validation. Future field studies will be of significantly increased value if they attempt to determine historical series of either natural recruitment or yellow and silver eel size structures. Despite these reservations, the model yields reasonable estimates of the expected recruitment and its variability. The bootstrap distribution shape of natural recruitment (Fig. 8) is highly skewed and lognormal-like in accordance with both empirical studies (Allen 1973; Hennemuth et al. 1980; Garrod 1983) and theoretical arguments (Ricker 1954; Walters and Hilborn 1976, Peterman 1978; Hollowed et al. 1987, Evans and Rice 1988; Armstrong and Shelton 1988; Fogarty et al. 1991; Shelton 1992) about the recruitment distribution of marine fishes.

The assumption of constant recruitment is, however, specific to this application, being a consequence of the relative scarcity of data actually available to fit the model. As a matter of fact, the set of equations that specify cohort dynamics has been derived with no reference to the time invariance of natural recruitment. The introduction of patterns or trends in recruitment is straightforward, as we have shown in the validation section where the contribution of a number of restocked fish cohorts has been explicitly considered. More generally, the model presented in this paper is quite flexible: survival, sexual-maturity and net-selectivity functions can be modified to satisfy more realistic assumptions or to test new hypotheses on the dynamics of the population at hand; ancillary data, such as sex ratios, can easily be used to improve the fitting of the model to data. Moreover, the model allows for the investigation of a variety of management policies, from fish restocking to the exploration of a range of fishing efforts and the use of different fishing gears, with size-dependent net selectivity, catch cost, and selling price being explicitly considered. Lastly, the computer code has been implemented on a workstation, much like a deterministic abundance model and is easily upgradable and portable to other hardware platforms with moderate effort.

We are quite confident that the conceptual framework used for modeling the specific case of European eel demography can be easily extended to a variety of other species in which plasticity of body growth leads to a wide spectrum of organism sizes within cohorts of individuals of the same age. Size dispersion over ages is remarkably important whenever success in reproduction, survival, predation liability, or any other trait happens to be affected by size rather than age. Therefore, differences in size among individuals of the same age should be explicitly acknowledged and accounted for, rather than ignored and averaged over. From a practical point of view, size determination involves simply weighing or measuring individual organisms, whereas age determination is more complicated and involves counting periodic marks of otoliths or scales. As a result, supplementing data on age structure with data on size structure comes at no cost and it is certainly wasteful to neglect these very useful data.

It should be finally noted that, while our model retains the power of more complex partial differential equation models to simulate continuous size distributions, the mathematical framework here derived allows for a straightforward extension to an individual-oriented formulation in which many different individuals, each with its own characteristics, are simulated simultaneously with a Monte-Carlo-like approach (De Angelis et al. 1993). In such a case the distribution of sizes can be derived as the sum of the simulation of many individuals. The demographic consequences of small population size, environmental stochasticity, and complex individual behaviors can be investigated provided Eqs. 7, 12, 13, 16, and 17 are replaced by their suitable individual-oriented counterparts, with growth factors and sexual maturation and survival probabilities being drawn for each individual from the respective probability density functions estimated on available data. Whether the individual-oriented approach, which is surely even more computer intensive than ours, can provide real advantages for fishery management is certainly an issue that deserves being debated and investigated.

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References

Allen, K.R. 1973. The influence of random fluctations in stock–recruitment relationships on the economic return from salmon fisheries, *In* B.B. Parrish [ed.] Fish stocks and recruitment. Rapp. P. V. Reun. Cons. Int. Explor. Mer 164: 350–359.

Armstrong, M.J., and P.A. Shelton. 1988. Bias in estimation of stock–recruit function parameters caused by nonrandom environmental variability. Can. J. Fish. Aquat. Sci. 45: 554–557.

Banks, H.T., L.W. Botsford, F. Kappel, and C. Wang. 1988. Modeling and estimation in size structured population models, pp. 521–591. *In* T.G. Hallam, L.J. Gross and S.A. Levin [ed.] Mathematical ecology. World Scientific, Singapore.

Banks, H.T., L.W. Botsford, F. Kappel, and C. Wang. 1991. Estimation of growth and survival in size-structured cohort data: an application to larval striped bass (*Morone saxatilis*). J. Math. Biol. 30: 125–150

Carrieri, A., G. Cavallini, I.M. Plazzi, and R. Rossi. 1992. Struttura della popolazione di anguille gialle ed argentine (*Anguilla anguilla* L.) nelle Valli di Comacchio (Biennio 1989–90). Ann. Univ. Ferrara (Nuova Ser.) Sez. 20 Biol. 2: 1–24.

Caswell, H. 1986. Life cycle models for plants. Lect. Math. Life Sci. 18: 171–185

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Mass.

Colombo, G. 1972*a*. Rassegna delle ricerche condotte nelle Valli da pesca dell'Alto Adriatico. Ann. Univ. Ferrara 1: 1–34

Colombo, G. 1972*b*. Primi risultati delle ricerche sulle residue Valli di Comacchio e piani delle ricerche future. Boll. Zool. 39: 471–478.

D'Ancona, U. 1959. Distribution of the sexes and environmental influence in the European eel (*Anguilla anguilla* (Linnaeus, 1758)): a suggestion to cope with it. Aquaculture, 9: 373–379.

D'Ancona, U. 1960. The life-cycle of the Atlantic eel. Symp. Zool. Soc. London, 1: 61–77.

DeAngelis, D.L. K.A.Rose, L.B. Crowder, E.A. Marschall, and D. Lika 1993. Fish cohort dynamics: application of complementary modeling approaches. Am. Nat. 142: 604–622.

Deevey, E.S. 1947. Life tables for natural populations animals. Q. Rev. Biol. 22: 283–314

Deriso, R.B., and A.M. Parma. 1988. Dynamics of age and size for a stochastic population model. Can. J. Fish. Aquat. Sci. 45: 1054–1068

Efron B. 1982. The jackknife, the bootstrap and other resampling plans. Society for the Industrial and Applied Mathematics, CBMS – Natl. Sci. Found. Monogr. Philadelphia, Pa.

Efron, B., and R. Tibshirani. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. Stat. Sci. 1: 54–77.

Evans, F.T., and J.C. Rice. 1988. Predicting recruitment from stock size without the mediation of a functional relation. J. Cons. Cons. Int. Explor. Mer 44: 111–122

Fogarty, M.J., M.P. Sissenwine, and E.B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine population. U.S. Energy Res. Dev. Idaho Oper. Off. Rep. TREE, 6: 241–246

Fournier, D.A., and I.J. Doonan. 1987. A length-based stock assessment method utilizing a generalized delay difference model. Can. J. Fish. Aquat. Sci. 44: 422–437

Garrod, D.J. 1983. On the variability of year-class strength. J. Cons. Cons. Int. Explor. Mer 41: 63–66.

Gatto, M., and R. Rossi. 1979. A method for estimating mortalities and abundances of the Valli di Comacchio eels. Mem. Ist. Ital. Idrobiol. Dott. Marco de Marchi 37(Suppl.): 107–114.

Gatto, M., E. Laniado, and R. Rossi. 1982. The management of eels in the Valli di Comacchio lagoons. *In* Proceedings of the International Symposium on Coastal Lagoons. SCOR/IABO/UNESCO, Bordeaux, France, 8–14 Sept. 1981. Oceanol. Acta, 5: 303–307.

Hennemuth, R.C., J.E. Palmer, and B.E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northwest Atl. Fish. Sci. 1: 101–111

Hollowed, A.B., K.M. Bailey, and W.S. Wooster. 1987. Patterns in recruitment of marine fishes in the Northeast Pacific Ocean. Biol. Oceanogr. 5: 99–131.

Johnson, N.L., and S. Kotz. 1970. Distributions in statistics: continuous univariate distribution. Houghton Mifflin Co., Boston, Mass.

Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. Ecology, 65: 1874–1884.

Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics, 21: 1–18.

Leslie, P.H. 1945. On the use of matrices in certain population mathematics. Biometrika, 33: 183–212.

Metz, J., and O. Diekmann. 1989. The dynamics of physiologically structured populations. Springer Lect. Notes Biomath. 68. Springer, Heidelberg, Germany.

Meyer, J.S., C.G. Ingersoll, L.L. McDonald, and M. Boyce. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology, 67: 1156–1166.

Nyman, L. 1972. Some effects of temperature on eel (*Anguilla*) behaviour. Rep. Inst. Freshwater Res. Drottningholm, 52: 90–102.

Pearl, R. 1928. The rate of living. Knopf, New York, N.Y.

Pelletier, D., and P. Gros. 1991. Assessing the impact of sampling error on model-based management advice: comparison of equilibrium yield per recruit variance estimators. Can. J. Fish. Aquat. Sci. 48: 2129–2139

Peterman, R.M. 1978. Testing for density-dependent marine survival in pacific salmonids. J. Fish. Res. Board Can. 35: 1434–1450.

Pinder, J.E., J.G. Wiener, and M.H. Smith. 1978. The Weibull distribution: a new method of summarizing survivorship data. Ecology, 59: 175–179.

Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling. 1988. Numerical Recipes in C. Cambridge University Press, Cambridge, Mass.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

Rossi, R. 1979. An estimate of the production of the eel population in the Valli di Comacchio (PO Delta) during 1974–1976. Boll. Zool., 46: 217–223.

Rossi, R., and G. Colombo. 1976*a*. Sex ratio, age and growth of silver eels in two brackish lagoons in the northern Adriatic. Arch. Oceanogr. Limnol., 18: 327–341.

Rossi, R., and G. Colombo. 1976*b*. Some investigations on growth of silver eels of North Adriatic lagoons. Boll. Pesca Piscic. Idrobiol. 31: 283–289.

Rossi, R., and G. Colombo. 1979. Some observations on age, sex and growth of silver eels (*Anguilla anguilla* L.) in northern Adriatic lagoons. Rapp. P.-V. Réun. Cons. Int. Explor. Mér 174: 64–69.

Rossi, R., and P. Franzoi. 1991. Pesca di ceche lungo le coste italiane nel periodo 1987–89. Boll. AIDA, 1: 15–17.

Rossi, R., A. Carrieri, P. Franzoi, and M. Bianchini. 1986. Freeze-branding in population assessment of the eel *Anguilla anguilla* (L.). Oebalia, 13: 15–25.

Rossi, R., A. Carrieri, P. Franzoi, G. Cavallini, and A. Gnes. 1987–1988. Eel population dynamics in the Comacchio lagoons. Oebalia, 15: 87–106.

Rossi, R., A. Carrieri, M.G. Rizzo, and M. Lucchini. 1988. Use of intensive rearing systems as back-up of lagoon aquaculture: an experience with the eel (*Anguilla anguilla* L.) in the Comacchio lagoons. Aquacult. Fish. Manage. 19: 47–53.

Sadler, K. 1979. Effects of temperature on the growth and survival of the European eel, *Anguilla anguilla* L. J. Fish Biol., 15: 499–507.

Schnute, J.T. 1981 A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38: 1128–1140

Schnute, J.T. 1987. A general fisheries model for size-structured fish population. Can. J. Fish. Aquat. Sci. 44: 924–940.

Schnute, J.T., L.J. Richards, and A.J. Cass. 1989*a*. Fish growth: investigations based on a size-structured model. Can. J. Fish. Aquat. Sci. 46: 730–742.

Schnute, J.T., L.J. Richards, and A.J. Cass. 1989*b*. Fish survival and recruitment: investigation based on a size-structured model. Can. J. Fish. Aquat. Sci. 46: 743–769.

Seber, G.A.F., and C.J. Wild. 1989. Non-linear regression. John Wiley & Sons, Inc., New York, N.Y.

Shelton, P.A. 1992. The shape of recruitment distribution. Can. J. Fish. Aquat. Sci., 49: 1754–1761

Sinko, J., and W. Streifer. 1967. A new model for age–size structure for a population. Ecology, 48: 910–918.

Tesch, F.W. 1977. The eel biology and management of anguillid eels. Chapman and Hall, London.

Vøllestad, L.A. 1986*a*. Growth and production of female yellow eels, *Anguilla anguilla* (L.), from brackish water in Norway. Vie Milieu, 36: 267–271.

Vøllestad, L.A. 1986*b*. Temperature-dependent activity of brackish yellow eels, *Anguilla anguilla* (L.). Aquacult. Fish. Manage. 17: 201–205.

Vøllestad, L.A. 1992. Geographic variation in age and length at metamorphosis of maturing European eel: environmental effects and phenotypic plasticity. J. Anim. Ecol. 61: 41–48.

Vøllestad, L.A., and B. Jonsson. 1986. Life-history characteristics of the European eel *Anguilla anguilla* in the Imsa River, Norway. Trans. Am. Fish. Soc., 115: 864–871.

Vøllestad, L.A., and B. Jonsson. 1988. A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. J. Anim. Ecol. 57: 983–997.

Walsh, P.J., G.D. Foster, and T.W. Moon. 1983. The effects of temperature on metabolism of the American eel, (*Anguilla rostrata* (LeSueur)): compensation in the summer and torpor in the winter. Physiol. Zool. 56: 532–540.

Walters, C.J., and R. Hilborn. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33: 145–159.

Appendix 1.

Glossary of functions and parameters. This appendix describes and summarizes all notation used in the paper. Numbers in parentheses refer to equations where the symbol is defined or used.

A	cross section of a yellow eel (19)
A_{med}	semisaturation constant of the net selectivity function (19)
B	number of bootstrap replicates
b, c	scale and shape parameters of the Weibull mortality function $Q(x)$ (15)
F, M	superscripts specifying parameters for females and males
g	growth factor (a random variable log-normally distributed with unitary mean and variance σ_g^2) (7)
k	slope parameter of the Von Bertalanffy growth curve (8)
l	eel body size

l^+	eel size in autumn (given its size in the previous spring was l)
l_{max}	maximum body size
$L(x)$	mean body size at age x
L_∞	asymptotic body size (8)
L_0	mean body size of elvers at age 0 (8)
m	number of eels in the sample
n	power of the objective function (25) in the estimation procedure
$Q(x)$	probability of dying before age x
$r(l)$	probability distribution function of recruitment with respect to size
$R(t)$	number of elvers recruited in year t
R_a	expected number of elvers
R_w	expected biomass of newly recruited individuals (28)
$S(x,l,t)$	expected number of silver eels of age x and size l in year t
$s(x,l,t)$	probability that an elver recruited in year $t - x$ will be an x-year-old silver eel of size l in year t
t	beginning of year t (spring)
t^+	beginnig of the fishing season of year t (late Autumn)
$w(l)$	generic length–weight relationship
$w_Y(l)$, $w_S(l)$	length–weight relationship for yellow eel and silver eels, respectively (26–28)
x	age of an eel in spring
x^+	age of an eel in autumn
x_0	age at recruitment
x_{max}	maximum age
$Y(x,l,t)$	expected number of yellow eels of age x and size l in year t
$y(x,l,t)$	probability that an elver recruited in year $t - x$ will be an x-year-old yellow eel of size l in year t
α, β	parameters of the length–weight relationship (21)
$\gamma(l)$	fraction of yellow eels of size l undergoing metamorphosis to the silver stage (16–18)
γ_{max}	maximum rate of metamorphosis (18)
δ	eel specific weight (20)
ε_t	random factor, with unitary geometric mean, that modulates the mean recruitment abundance R
ζ	slope parameter of the net selectivity function (19)
η	slope parameter of the metamorphosis function $\gamma(l)$ (18)
θ_j	jth unknown parameter ($j = 1, 2, \ldots, 8$) of the demographic model
$\theta^*_{i,j}$	value of the jth parameter ($j = 1, 2, \ldots, 8$) estimated from the ith bootstrap replicate ($i = 1, 2, \ldots, 1000$)
θ^B_j	mean value of the jth parameter ($j = 1, 2, \ldots, 8$) estimated from its bootstrap distribution
θ^{true}_j	true value of θ_j
θ^{all}_j	full sample estimate of jth parameter for the original data set
θ^{B-adj}_j	bias-adjusted bootstrap estimate of θ^{true}_j
$\Theta(x,t)$	expected number of yellow eels of age x in year t (1)
Λ	$= L_\infty(1 - e^{-k})$ (11)
λ	semi-saturation constant of the metamorphosis function $\gamma(l)$ (18)
$\Xi(\theta_j, j = 1, 2, \ldots, 8)$	objective function used in the estimation procedure (25)
$\pi^Y_l(t)$	frequency distribution of sizes of yellow eels in year t (5, 24)
$\pi^{Y^*}_l(t)$	frequency distribution of sizes of yellow eels captured in fyke nets in year t (5, 24)
$\pi^S_l(t)$	frequency distribution of sizes of silver eels in year t (5, 24)
ρ	$= e^{-k}$ (11)
σ^2_g	variance of g (9)
$\sigma^2_{\ln(g)}$	variance of $\ln(g)$ (8)
$\sigma(x)$	survival between age x and age x^+ (15)
$\Phi(A)$	net selectivity as a function of eel cross section (19)
$\Psi(t)$	expected number of yellow eels in the lagoon in year t (2)

Accounting for individual variability in the von Bertalanffy growth model

You-Gan Wang and Mervyn R. Thomas

Abstract: Estimation of von Bertalanffy growth parameters has received considerable attention in fisheries research. Since Sainsbury (1980, Can. J. Fish. Aquat. Sci. 37: 241–247) much of this research effort has centered on accounting for individual variability in the growth parameters. In this paper we demonstrate that, in analysis of tagging data, Sainsbury's method and its derivatives do not, in general, satisfactorily account for individual variability in growth, leading to inconsistent parameter estimates (the bias does not tend to zero as sample size increases to infinity). The bias arises because these methods do not use appropriate conditional expectations as a basis for estimation. This bias is found to be similar to that of the Fabens method. Such methods would be appropriate only under the assumption that the individual growth parameters that generate the growth increment were independent of the growth parameters that generated the initial length. However, such an assumption would be unrealistic. The results are derived analytically, and illustrated with a simulation study. Until techniques that take full account of the appropriate conditioning have been developed, the effect of individual variability on growth has yet to be fully understood.

Résumé : L'estimation des paramètres de croissance de von Bertalanffy reçoit depuis un certain temps une attention considérable dans le domaine de la recherche halieutique. Depuis l'article de Sainsbury (1980, J. can. sci. halieutiques aquat. 37 : 241–247), une bonne partie de ces travaux ont été axés sur la façon de prendre en compte la variabilité individualle dans les paramètres de croissance. Dans notre étude, nous démontrons que la méthode de Sainsbury et ses dérivés, appliqués à l'analyse des données de marquage, ne permettent généralement pas de bien rendre compte de la variabilité individuelle de croissance, de sorte que les estimations des paramètres ne sont pas cohérentes. En effet, le biais ne tend pas vers zéro à mesure que la taille de l'échantillon va vers l'infini. Ce biais, similaire à celui de la méthode de Fabens, vient du fait que ces méthodes ne prennent pas comme base d'estimation les espérances conditionnelles appropriées. De telles méthodes ne peuvent convenir que dans l'hypothèse où les paramètres de croissance individuelle qui produisent l'augmentation de longueur seraient indépendants des paramètres de croissance qui ont produit la longueur initiale. Une telle hypothèse est toutefois irréaliste. Les résultats sont obtenus par analyse et illustrés par une simulation. En l'absence de techniques prenant pleinement en compte le conditionnement approprié, on ne pourra élucider parfaitement l'effet de la variabilité individuelle sur la croissance.

[Traduit par la Rédaction]

Introduction

The von Bertalanffy equation has often been used to describe the growth of fish and other marine animals. The equation describes the relationship between age (a) and length (l) as

$$[1] \quad l(a) = L_\infty(1 - e^{-K(a-T_0)})$$

in which L_∞, K, T_0 are growth parameters.

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Tag–recapture is a common method for estimating growth parameters (L_∞, K), especially for species that cannot be aged directly. In tag–recapture studies, the length at capture (l), interval between release and recapture (t), and growth increment during the time interval (I) are recorded. If no information is available for the age at capture, tag–recapture data provide no information to allow estimation of the parameter T_0. The parameter T_0 can, therefore, be fixed at zero, without consequences for estimation of the parameters L_∞ and K (Sainsbury 1980).

Fabens (1965) derived an expression for I as a function of l and t:

$$[2] \quad I = (L_\infty - l)(1 - e^{-Kt})$$

Estimation of the growth parameters, based on Eq. 2 and using ordinary least squares, is known as the Fabens method. The Fabens method assumes that the parameters in Eq. 2 are the same for all individuals, i.e., each individual

follows an identical von Bertalanffy growth curve. Many authors have recognised that this assumption is unrealistic (Sainsbury 1980; Kirkwood and Somers 1984; Hampton 1991; Xiao 1994), and that the Fabens method leads to inconsistent estimators. These authors have attempted to modify the Fabens method by incorporating individual variability in the parameters of Eqs. 1 and 2.

Generalizations of Sainsbury's (1980) method continue to receive the attention of researchers (Hampton 1991; Xiao 1994). It is possible to characterize the relative performance of these techniques under a wide range of conditions. The objective of this paper, however, is to show that the individual variability in growth is not accounted for in the method of Sainsbury (or its derivatives), and that they are not markedly different from the Fabens method itself. For the convenience of further discussion and introducing the necessary notation, we first present a brief summary of Sainsbury's (1980) and Kirkwood and Somers' (1984) methods, and then analyse both methods based on the expected increments for an individual and for the population. We show that these methods and their derivatives do not properly take account of individual variability in growth parameters (and are therefore inconsistent). Ironically, these methods would be consistent (asymptotically unbiased) only if the growth parameters for any individual vary randomly over time. We illustrate this with a simulation study. Finally we indicate some possible directions for future research to account for individual variability in growth.

Throughout this paper, we will denote Fabens (1965) by F, Sainsbury (1980) by S, Kirkwood and Somers (1984) by K&S, Hampton (1991) by H, and Xiao (1994) by X.

Analysis of existing methods

S, K&S, and X make the following assumptions in their models:

(1) Each animal has its own triplet von Bertalanffy parameters, L_∞, K, T_0, that are retained throughout its life.

(2) The conditional distribution of K and L_∞ is identical over the age or length range considered.

Here L_∞ and K are regarded as random variables with means $\bar{L}_\infty$ and $\bar{K}$ and variances $\sigma^2_{L_\infty}$ and σ^2_K, respectively.

Suppose that the mean length of the population at release is $\bar{l}$, with individual lengths represented by the random variable l. The mean increment in length, during the time interval t and conditional on the initial mean length $\bar{l}$ is given by $E_p[l|\bar{l},t]$, where the subscript p indicates that the expectation is taken over the entire population. Under assumption 2, we may write:

$$[3]\quad E_p[l|\bar{l},t] = \bar{L}_\infty - \bar{l} + \bar{l}\,E[e^{-Kt}] - E[L_\infty e^{-Kt}]$$

$$V_p[l|\bar{l},t] = E[(\bar{L}_\infty - \bar{l})^2(1 - e^{-Kt})^2] - (E_p[l|\bar{l},t])^2$$

The evaluation of these expectations depends on the distributions of K and L_∞. The methods of S, K&S, H, and X are based on different assumptions about the distribution of (K, L_∞), hence leading to different expressions for the expectations and variances.

Kirkwood and Somers (1984)

K&S assume that L_∞ is a normal random variable, but that K is fixed (hence $K = \bar{K}$). Their expressions for the conditional mean and variance of l are

$$[4]\quad E_p[l|\bar{l},t] = (\bar{L}_\infty - \bar{l})(1 - e^{-\bar{K}t})$$

$$[5]\quad V_p[l|\bar{l},t] = \sigma^2_{L_\infty}(1 - e^{-\bar{K}t})^2$$

K&S constructed a likelihood function based on a normal model, with mean and variance given by Eqs. 4 and 5, and proposed use of maximum likelihood estimation. This method, in fact, is the same as the weighted least squares (weighed by the inverse of the variance). In the special case when t is constant for all individuals, their maximum likelihood approach is equivalent to the Fabens method.

Sainsbury (1980)

Sainsbury provided a general expression for the mean and variance of l, conditional on $\bar{l}$ and t, under the assumption that K and L_∞ are independent. He proposed a normal distribution for L_∞ and a gamma distribution for K. This generates the following expressions for the conditional mean and variance of l:

$$E_p[l|\bar{l},t] = (\bar{L}_\infty - \bar{l})\left[1 - \left(1 + \frac{\sigma^2_K t}{\bar{K}}\right)^{\frac{-\bar{K}^2}{\sigma^2_K}}\right]$$

$$V_p[l|\bar{l},t] = k_1\sigma^2_{L_\infty} + k_2(\bar{L}_\infty - \bar{l})^2$$

where

$$k_1 = 1 - 2\left(1 + \frac{\sigma^2_K t}{\bar{K}}\right)^{\frac{-\bar{K}^2}{\sigma^2_K}} + \left(1 + \frac{2\sigma^2_K t}{\bar{K}}\right)^{\frac{-\bar{K}^2}{\sigma^2_K}}$$

and

$$k_2 = \left(1 + \frac{2\sigma^2_K t}{\bar{K}}\right)^{\frac{-\bar{K}^2}{\sigma^2_K}} - \left(1 + \frac{\sigma^2_K t}{\bar{K}}\right)^{\frac{-2\bar{K}^2}{\sigma^2_K}}$$

Sainsbury develops estimates for the growth parameters based on an approximating normal likelihood, with mean and variance given above. As he points out, the exact distribution of l will not be normal, but the approximation should be reasonable for modest sample sizes (larger than 100).

The methods of S and K&S (and their derivatives) assume that Eq. 3 is the expected growth increment for an individual, conditional on length at tag $\bar{l}$ and time at liberty t. In fact, the expectations are taken over the entire population, and they are generally different from the expectation for an individual. We will demonstrate that use of Eq. 3 to represent the conditional growth increment for a given animal fails to take proper account of individual variability, and is responsible for the inconsistency in the techniques of S, K&S, and their derivatives. We now present some analytical results and illustrate the difference between these two expectations.

Expected increment for an individual

As discussed above, the existing methods rely on the expected increment for the population (a group of animals). We now introduce the counterpart of $E_p[l|\bar{l},t]$, the expected increment for an individual, which has not been given as much attention as it should have in the analysis of tagging data. To obtain the expected increment for an individual of initial length l, we need to calculate the conditional expectation:

$$[6] \quad E_i[l|l,t] = E_i[L_\infty|l,t] - l + l\,E_i[e^{-Kt}|l,t] - E_i[L_\infty e^{-Kt}|l,t]$$

where the subscript i indicates that the expectation is for an individual animal, not over the entire population. In general, evaluation of the expectation in Eq. 6 is complex and requires knowledge of the distributions of age (t) and L_∞. Inspection of Eqs. 3 and 6 shows that the expectation for the individual increment will be the same as that for the population increment only when K and L_∞ are independent of l. We illustrate their difference for the simple case of constant K (i.e., $K = \bar{K}$), where

$$E_i[l|l,t] = E_i[L_\infty|l,t] - l + le^{-Kt} - E_i[L_\infty|l,t]e^{-Kt}$$

To evaluate $E_i[L_\infty|l,t]$, we introduce the quantity $\rho = 1 - e^{-KA}$ where A is the age at release. If ρ and L_∞ are independent (i.e., an animal's age at release is independent of its maximum attainable size), using elementary distribution theory, we may write (Wang et al. 1995):

$$[7] \quad E_i[L_\infty|l,t] = \frac{\int g(l/x)f(x)\,dx}{\int g(l/x)f(x)/x\,dx}$$

where $g(x)$ and $f(x)$ are the density functions of ρ and L_∞, respectively. From this equation, assumption 2 cannot, in general, be true for individuals, because the conditional expectation of L_∞ is dependent on l.

The difference between $E_i[l|l,t]$, and $E_p[l|\bar{l},t]$ is illustrated in Fig. 1 as a function of initial length. These expectations are calculated by assuming that L_∞ is normally distributed with a mean of 100 and a standard deviation of 10, K is a constant of 0.5, and time at liberty is fixed at 1 year. The age at release A was assumed to be uniformly distributed over four different ranges, (1,2), (0.5, 2.5), (1.0, 1.5), and (2.0, 2.5). These four distributions correspond to four cases: (1) the length at release has a moderate range with a moderate mean (Fig. 1*a*); (2) the length at release has a wide range with a moderate mean (Fig. 1*b*); (3) the length at release has a small range with a moderate mean (Fig. 1*c*); and (4) the length at release has a large mean (Fig. 1*d*). Some simulated increments of individuals are also plotted to represent the ranges and variations of the lengths at release under different assumptions. As we can see, the population expectation, $E_p[l|\bar{l},t]$, is always linear in l, while the expectation for an individual, $E_i[l|\bar{l},t]$, shows marked nonlinearity with an intercept around the mean initial length. In the cases of Figs. 1*b*–1*d*, the expected increment for an individual is almost linear in the observed range of the lengths at release. In Fig. 1*b*, the conditioning has little effect on the expected mean because of rather large uncertainties in age, while in Figs. 1*c* and 1*d*, the expected increment for an individual increases in the length at release while the expected increment for the population always decreases. Perhaps, Fig. 1 is the more representative of real data. Note that these simulated data are based on the assumption of constant time at liberty. In practice, time at liberty is more likely to vary and thus more variations in the observed length increments will be expected.

The expected increment for an individual is smaller (larger) than that for the population for those with smaller (larger) length at release. Consequently, overestimation of $\bar{L}_\infty$ and underestimation of $\bar{K}$ will occur for the method of F. In general, the difference between K&S, S, and the classical method F is only due to different weighting functions and nonlinearlity in K and, therefore, is not fundamental. So we will expect similar performance from these three methods.

Simulation study

Two sets of simulations were performed to demonstrate that (1) the estimates of F, K&S, and S are biased under assumption 1, and (2) the bias diminishes when the growth parameters of individuals are assumed to change from time to time randomly and independently, i.e., assumption 2 holds for all individuals. Subsequently, we will refer to the case of the first simulation study as the model with stable growth parameters and the case of the second study as the model with changing growth parameters.

Note that the units for time and length are not given here, because they can be chosen as any sensible time and metric units. For instance, the time units can be year, month, or even a quarter of a year, and the length unit can be centimetres, or 0.5 inch, etc. The unit for K is always the inverse of the time unit.

In the first study, we generated data sets by sampling animal age at capture (A) and growth parameters (L_∞, K). Length at release was calculated from these random variables. Time at liberty (between release and recapture) was then sampled, and length increment at recapture was finally evaluated from the time at liberty and the original growth parameters.

A different sampling procedure was adopted for the second study. Once again, age at release, L_∞, and K were sampled; length at release was calculated; time at liberty was sampled; and length increment was calculated from length at release, time at liberty, and the growth parameters L_∞ and K. But this time K and L_∞ were resampled from their distributions. Consequently, the growth parameters used to calculate the growth increment during the interval between release and recapture were independent of those used to calculate growth up to the time of release. Therefore, the values of L_∞, and K that determine the increment are independent of the value of l. Therefore, the expected increment for the individual (Eq. 6) is the same as that for the population (Eq. 3). Under this circumstance we expect the techniques of F, S, and K&S to perform well.

Age at release (A) was sampled from a uniform distribution on (1, 2), and time at liberty was sampled as 0.1 plus an exponential random variable with a mean of 1. In

each study, we examined two cases: (1) only L_∞ varies among individuals while K is a constant, and (2) both L_∞ and K vary among individuals. In both cases, L_∞ was sampled from a normal distribution with a mean of 100 and a standard deviation of 10. In the first case, K was assumed to be a constant of 0.5, and in the second case, K was sampled from a gamma distribution with a mean of 0.5, and a standard deviation of 0.158 ($\alpha = 10$, $\beta = 0.05$, where the probability density function is given by $x^{\alpha-1}\, e^{-x/\beta}/(\beta^\alpha \Gamma(\alpha))$). One thousand data sets, each with 100 recaptures, were generated in each case of the two studies.

Each data set was analysed using the methods of F, S, and K&S, and 1000 sets of estimated parameters were obtained for each method. Results of both simulations are summarised in Table 1. Means and standard deviations of the estimates of L_∞ and K are given for each estimation method, based on stable growth parameters (i.e., as in the first set of simulations, not resampled) and based on changing growth parameters (from the second set of simulations, resampled).

The growth curve is always determined by the joint effect of L_∞ and K. One of the indices that combine the two parameters is the growth performance index $\lambda = L_\infty K/2$, the instantaneous growth rate at $L_\infty/2$ (Dall et al. 1990; Milton et al. 1993; see Discussion). This index also takes into account some of the wide variation in the estimates of L_∞ and K.

In the case of stable growth parameters, the estimators for both L_∞ and K show substantial biases. The biases become much larger when both L_∞ and K are variable (≥40%) compared with the case when only L_∞ is variable. For the index λ, the bias is still as high as 20% when only L_∞ is variable, and up to 43% when both L_∞ and K are variable. However, when the growth parameters are resampled, the biases diminish to no more than 6% for all the estimates, and the biases become much smaller when K is a constant. There appears to be no clear evidence of bias for the estimates of L_∞, K, and λ from the resampled data, using the methods of F and S.

The conclusion to be drawn from this simulation exercise is that these methods may produce substantial bias when individual variability in growth exists, and the bias is negligible when the individual growth parameters change independently from time to time or when the growth parameters are the same for all individuals.

Discussion

In general, an efficient estimation method should make use of length at release and length at recapture equally and take into account the correlation between them for each individual. The correlation is obviously due to the fact that both lengths are generated from the same growth parameters and initial age. The methods we discussed above can be easily modified by expressing the expected increment in terms of length at recapture rather than length at release. Such a simple modification (all the underlying assumptions remain the same) will result in different estimates, suggesting the inefficiency of these methods.

K&S noted that their method is effectively the same as a weighted least squares method while the Fabens method is the ordinary least squares one. Therefore, it is not surprising that their method is inconsistent (a precise statistical term that for our purposes means that the bias in estimates tend to zero as the sample size tends to infinity). Maller and DeBoer (1988) investigated the performance of the F and K&S techniques and provided some analytical results in the case of constant time at liberty. They also concluded that, in general, no weighted least squares analysis of Eq. 2 (in which the weights do not depend on the unknown age) can produce consistent estimates.

The weakness in the approaches of S and K&S is that these methods are based on the population expectation of growth increment as given by Eq. 3, rather than on the expected growth increment for the individual. Figure 1 shows that, in general, there may be marked differences between the population expectation of increment (which is linear in initial length) and the conditional expectation of increment for an individual (which shows marked nonlinearity in initial length).

The difference between the expected increment for an individual and for the population may be negligible when its length at release, l, is close to the mean length of the population at the time of release. However, when the distribution of age at release (A) has a small range, the expected increment for an individual becomes an increasing function of l, especially when A is the same for all fish released, the expected increment for an individual will be proportional to l and very different from the expected increment for the population (cf. Fig. 1*c*). It appears that the difference between these two expectations may become ignorable when the distribution of age (length) at release is widely spread out (cf. Fig. 1*b*). This is because conditioning has little effect on the expected increment when the uncertainty in A is so large.

Assumption 1 is a fundamental requirement of methods that attempt to account for individual variability in growth parameters. We have seen that this assumption leads to dependence between L_∞ and length at release. That is, for an individual animal the conditional expectation of L_∞ given l is not constant (Eq. 7). The conditional expectation of L_∞ for an individual, in general, is difficult to derive, and it depends on the age distribution of the population. It is, therefore, tempting to base the estimation on the population expected increment, which is easy to derive and does not depend on the age distribution.

Merely considering L_∞ and K to be random in the increment Eq. 2 does not properly account for individual variability in growth. Ignoring the conditioning of expected increment on length, l, is equivalent to assuming that there is no relationship between the value of l and the values of L_∞ and K during the period at liberty, and, hence, no relationship between the values of K and L_∞ at release from which l was generated and those during the period at liberty. In our simulation, we deliberately violated assumption 1 by resampling values of L_∞ and K, and indeed, only very small biases in the estimates were observed. This is because if we assume that the growth parameters for an individual are independent from time to time, its expected increment will be the same as that for the population, and these methods will be appropriate. The effect of

Fig. 1. Expected length increments over 1 year for an individual and the population at different initial lengths. The observed (simulated) individual increments were superimposed. The underline distribution of L_∞ is normal with mean 100 and standard deviation 10 while K is a constant of 0.5. The units for time and length can be chosen at discretion. The age at release is assumed to be uniformly distributed between one and two. The age at release, A, is taken to be uniformly distributed on different ranges: (*a*) $A \sim U(1.0, 2.0)$; (*b*) $A \sim U(0.5, 2.5)$; (*c*) $A \sim U(1.0, 1.5)$; and (*d*) $A \sim U(2, 2.5)$.

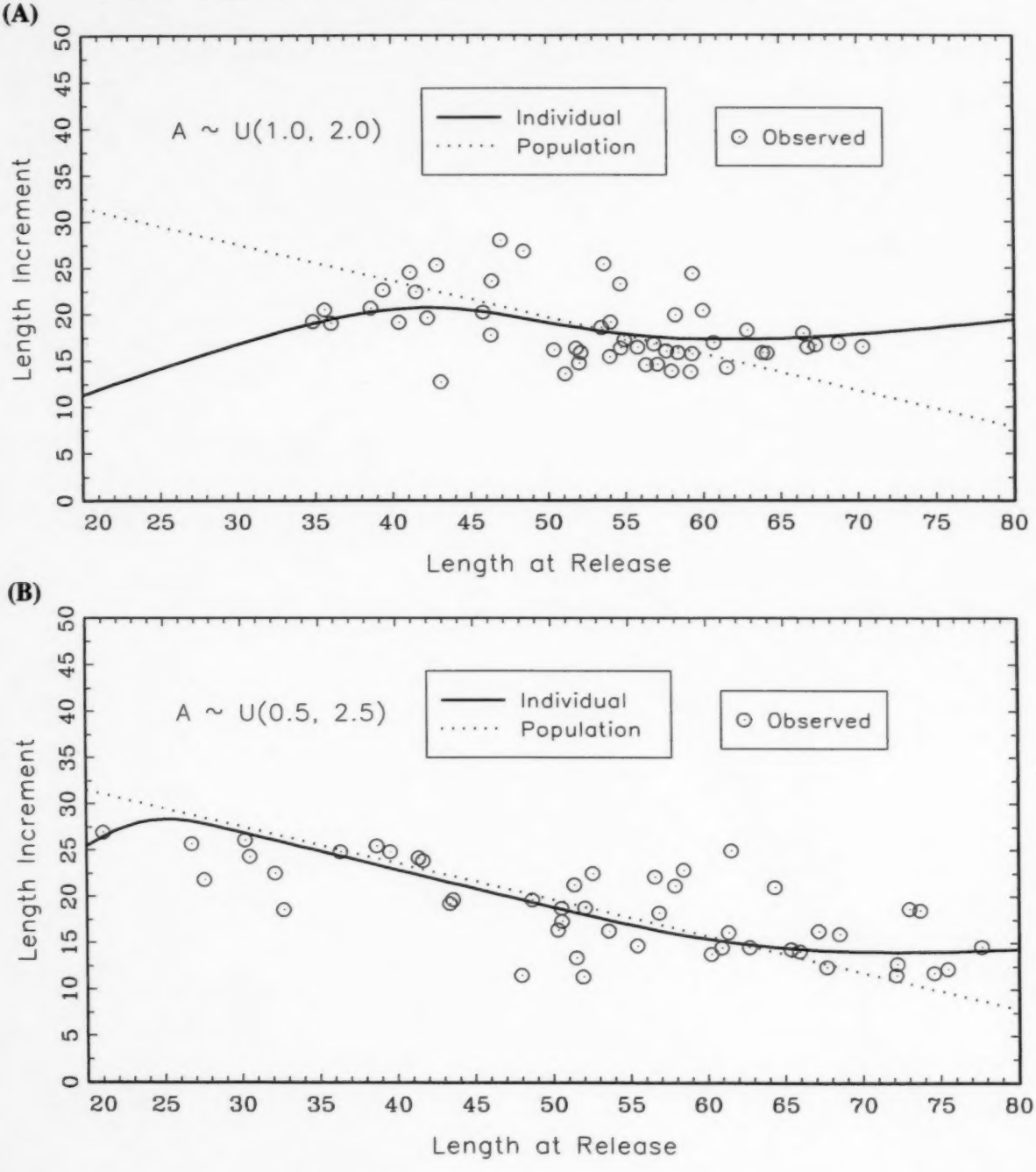

Fig. 1 (*concluded*).

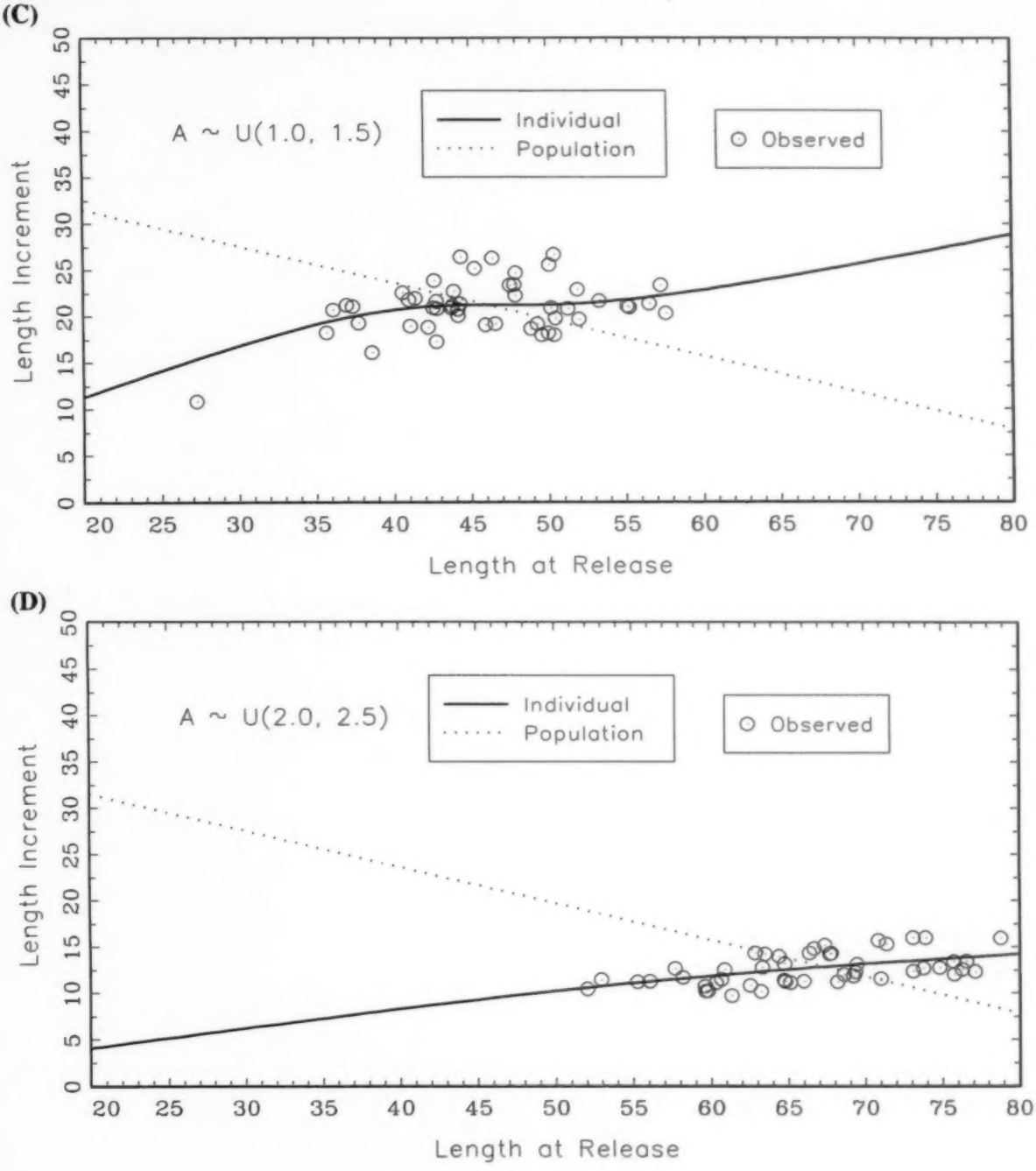

Table 1. Mean, standard deviation (in parentheses), and relative error (percent) of $\bar{L}_\infty$, $\bar{K}$, and λ estimated by three methods.

Methods	L_∞	Error (%)	K	Error (%)	λ	Error (%)
Stable growth parameters						
Only L_∞ variable						
Fabens	112.7 (9.5)	12.7	0.36 (0.07)	−28.2	19.9 (2.4)	−20.4
Kirkwood and Somers	121.0 (8.3)	21.0	0.33 (0.04)	−35.0	19.5 (1.4)	−21.4
Sainsbury	121.0 (8.3)	21.0	0.33 (0.04)	−34.8	19.5 (1.4)	−21.8
Both L_∞ and K variable						
Fabens	140.4 (35.4)	40.4	0.21 (0.06)	−57.9	14.0 (1.9)	−43.9
Kirkwood and Somers	204.2 (59.1)	104.3	0.14 (0.04)	−72.2	13.2 (1.2)	−47.2
Sainsbury	204.3 (143.5)	104.3	0.15 (0.05)	−69.9	13.6 (1.5)	−45.7
Changing growth parameters						
Only L_∞ variable						
Fabens	100.9 (5.4)	0.9	0.50 (0.07)	−0.5	24.9 (2.5)	−0.4
Kirkwood and Somers	100.3 (3.7)	0.3	0.50 (0.05)	−0.1	25.0 (1.5)	−0.1
Sainsbury	100.7 (3.8)	0.7	0.50 (0.05)	−0.1	24.8 (1.5)	−0.6
Both L_∞ and K variable						
Fabens	99.4 (5.1)	−0.6	0.50 (0.08)	0.2	24.7 (2.6)	−1.1
Kirkwood and Somers	97.6 (4.1)	−2.4	0.53 (0.07)	6.0	25.8 (2.3)	3.0
Sainsbury	100.4 (4.1)	0.4	0.50 (0.06)	0.0	25.0 (2.0)	0.0

Note: The true values of $\bar{L}_\infty$, $\bar{K}$, and λ are 100, 0.5, and 25, respectively. These results are based on 1000 simulations, each with 100 recaptured fish.

individual variability examined by S and X is therefore only due to the nonlinearlity in growth parameters. In the simulation analysis of H, the values of l were fixed, which is equivalent to the case of changing growth parameters. Therefore, his analysis is virtually invalid. The conclusion to be drawn here is that the existing methods developed in fisheries research do not account for the individual variability in growth for tagging data.

For the more realistic assumption (strong dependence over time of the growth parameters for an individual) these methods give inconsistent estimates. The size of the bias does not decrease with sample size, and these methods should not then be used when individual variability in growth exists. S did realise these problems, as pointed out in his discussion, and his analysis should be regarded as a "first analysis" on individual variability. K&S were also well aware that their method was based on population expectation, which they regarded as an approximation to the relevant conditional expectation. What is perhaps surprising is how poor the approximation can be.

One might argue that growth of fish probably depends on environmental factors, and hence, it is not absurd to assume changing growth parameters in the growth model when the environmental inputs are unknown. Perhaps it is reasonable to assume that, for each fish, L_∞ is genetically determined and retained throughout its life and K, which measures the growth rate, is either environmentally determined or constant if the environmental factors are stable over the period considered (Cloern and Nichols 1978; McCauley and Kilgour 1990).

The two growth parameters, as pointed out by Kingsley (1980), in general, measure two different characteristics of growth, corresponding to the two axes of the growth curve. Apparently, the objective of the parameter estimation is not to estimate these two parameters but to predict the growth rate. It is possible that biased estimates of L_∞ and K may result in a reasonable fit of the underlying growth curve within the age or length range of interest. Therefore, it is of interest to examine the effect of the estimates of L_∞ and K on predicting the growth rate. In addition to the estimates of L_∞ and K, we also investigated the growth performance index λ, the instantaneous growth rate at half the maximum length. This index combines the effect of both parameters and gives a different description of the growth characteristics. Apart from the index λ discussed here, the mean lengths at certain ages can also be used to assess the overall growth estimation of a method (Francis 1988). Nevertheless, our simulation study (Table 1) clearly demonstrated the problems in these methods.

The problems with these methods are retained by all those approaches which have been derived from them (H and X). A number of possible generalizations of these techniques could be explored (for example dealing with multiple recaptures). However, these generalizations would suffer from the same problems.

We believe that further research should be directed away from generalisation of the S and K&S techniques, and towards fully conditional procedures (Palmer et al. 1991; Wang et al. 1995). These fully conditional techniques are no more difficult to implement than the methods of S and K&S. Further generalization is possible to incorporate environmental inputs, seasonality, and measurement error. The nonlinear random coefficients model of Palmer et al. (1991) is computationally expensive, but useful for

combining data sets with multiple recaptures. Further investigation through the Gibbs Sampler (Gilks et al. 1994) to reduce the complexity is needed. The Gibbs sampler also provides a vehicle for developing more ambitious models, incorporating measurement error with autoregressive structure and individual variability.

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References

Cloern, J.E., and F.H. Nichols. 1978. A von Bertalanffy growth model with a seasonally varying coefficient. J. Fish. Res. Board Can. 35: 1479–1482.

Dall, W.D., B.J. Hill, P.C. Rothlisberg, and D.J. Staples. 1990. Biology of the Penaeidae. *In* Advances in the Marine Biology. Vol. 27. *Edited by* J.H.S. Blaxter and A.J. Southward.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth, 29: 265–289.

Francis, R.I.C.C. 1988. Are growth parameters estimated from tagging and age–length data comparable? Can. J. Fish. Aquat. Sci. 45: 936–942.

Gilks, W.R., A. Thomas, and D.J. Speigelhalter. 1994. A language and program for complex Bayesian modelling. Statistician, 43: 169–177.

Hampton, J. 1991. Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. Fish. Bull. U.S. 89: 577–590.

Kingsley, M.G.S. 1980. von Bertalanffy growth parameters. Trans. Am. Fish. Soc. 109: 252–253.

Kirkwood, G.P., and I.F. Somers. 1984. Growth of the two species of tiger prawn, *Penaeus esculentus* and *Penaeus semisulcatus*, in the western Gulf of Carpentaria. Aust. J. Mar. Freshwater Res. 35: 703–712.

Maller, R.A., and E.S. deBoer. 1988. An analysis of two methods of fitting the von Bertalanffy curve to capture–recapture data. Aust. J. Mar. Freshwater Res. 39: 459–466.

McCauley, R.W., and D.M. Kilgour. 1990. Effect of air temperature on growth of largemounth bass in North America. Trans. Am. Fish. Soc. 119: 276–281.

Milton, D.A., S.J.M. Blaber, and N.J.F. Rawlinson. 1993. Age and growth of three species of clupeids from Kiribati, tropical central south Pacific. J. Fish Biol. 43: 89–108.

Palmer, M.J., B.F. Phillips, and G.T. Smith. 1991. Application of non linear models with random coefficients to growth data. Biometrics, 47: 623–635.

Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. 37: 241–247.

Wang, Y.G., M. Thomas, and I.F. Somers. 1995. A maximum likelihood approach for estimating growth from tag–recapture data. Can. J. Fish. Aquat. Sci. 52: 252–259.

Xiao, Y. 1994. von Bertalanffy growth models with variability in, and correlation between, k and L_∞. Can. J. Fish. Aquat. Sci. 51: 1585–1590.

Production of germline transgenic Pacific salmonids with dramatically increased growth performance

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Abstract: Transgenic Pacific salmon have been produced by microinjection of a DNA construct consisting of chinook salmon (*Oncorhynchus tshawytscha*) growth hormone sequences driven by an ocean pout (Macrozoarces americanus) antifreeze protein promoter. This construct was retained in approximately 4% of fish derived from injected eggs, and resulted in dramatic enhancement of growth relative to controls. For coho salmon (*O. kisutch*) at 15 months of age, the average size of transgenic fish was more than 10-fold that of controls, with the largest fish more than 30-fold larger than nontransgenic siblings. Dramatic growth enhancement was also observed in transgenic rainbow trout (*O. mykiss*), cutthroat trout (*O. clarki*), and chinook salmon using this same gene construct. Transgenic coho salmon underwent precocious parr–smolt transformation during their first fall, approximately 6 months in advance of their nontransgenic siblings. At 2 years of age, five male transgenic coho salmon became sexually mature, and four of these transmitted the gene construct to sperm, the negative fish being transgenic in blood but not fin tissue. These results show that while some fish are mosaic for the gene construct in different tissues, most are transgenic in both germline and somatic tissue.

Résumé : Des saumons du Pacifique transgéniques ont été produits par microinjection d'un construit d'ADN formé de séquences d'hormone de croissance de saumon quinnat (*Oncorhynchus tshawytscha*) régulées par un promoteur de protéine antigel de la loquette d'Amérique (*Macrozoarces americanus*). Le construit a été conservé par 4% environ des poissons obtenus des oeufs injectés et a donné lieu à une augmentation extrêmement importante de la croissance de ces individus, par rapport aux témoins. Dans le cas du saumon coho (*O. kisutch*), la taille moyenne, après 15 mois, des poissons transgéniques était plus que 10 fois supérieure à celle des témoins, le plus gros poisson étant 30 fois plus gros que ses frères non transgéniques. Une très importante augmentation de la croissance a aussi été notée chez des truites arc-en-ciel (*O. mykiss*) et fardées (*O. clarki*) et des saumons quinnats porteurs du même construit. Les saumons cohos transgéniques ont présenté une smoltification hâtive au cours de leur premier automne, soit 6 mois plus tôt que les témoins. À 2 ans, cinq des cohos mâles transgéniques sont devenus matures et l'on a retrouvé, chez quatre d'entre eux, le construit dans les spermatozoïdes. Le cinquième poisson présentait le caractère transgénique dans ses tissus sanguins, mais non dans ceux de ses nageoires. Les résultats obtenus montrent que certains poissons ne présentent pas le construit dans tous leurs tissus, mais que la transgénie se manifeste tant dans les tissus germinaux que somatiques.
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Introduction

The development of transgenic fish has undergone intensive research since the first production of transgenic mammals over a decade ago. Transgenic fish are being developed for both academic and applied goals, allowing the creation of useful model systems as well as new genetic strains with improved characteristics for aquaculture (for reviews, see Maclean and Penman 1990; Chen and Powers 1990; Houdebine and Chourrout 1991; Fletcher and Davies 1991). Owing to the nature of many fish eggs (large with tough

chorions), a focus of many transgenic fish studies has been on the method of delivery of the DNA construct and the frequency of gene retention in P_1 individuals. Although many studies have shown the transient presence of the new genetic construct in microinjected fish eggs, only a few studies to date have observed phenotypic effects in transgenic fish as well as germline transmission (Dunham et al. 1992; Lu et al. 1992; Zhu 1992; Chen et al. 1993).

A variety of genes have now been introduced into fish with the goal of influencing traits such as growth, maturation, freezing tolerance, and disease resistance. It has been well documented that many fish species have a remarkable capacity for growth acceleration when treated with exogenous growth hormone (McLean and Donaldson 1993). Application of this technology has considerable potential for improving the efficiency of aquaculture by not only increasing growth but also reducing costs by improving feed conversion efficiencies. For these reasons, and because some mammalian studies with growth hormone (GH) transgenics resulted in significant growth effects, many transgenic fish studies have utilized mammalian or piscine GH genes. Studies demonstrating phenotypic consequences in GH transgenics in various fish species have observed different effects on performance, with growth enhancement ranging from 1.21- to more than 11-fold (Enikolopov et al. 1989; Zhang et al. 1990; Gross et al. 1992; Lu et al. 1992; Du et al. 1992; Dunham et al. 1992; Zhu 1992; Chen et al. 1993; Devlin et al. 1994). Such differences may arise from a combination of factors such as the biology of the different species, the structure of the gene construct (i.e., type of promoter and coding regions used), and the nature of the insertion (chromosome position, copy number, etc.). In the present investigation, we have produced germline transgenic Pacific salmon (coho salmon, *Oncorhynchus kisutch*; chinook salmon, *O. tshawytscha*), as well as transgenic rainbow (*O. mykiss*) and cutthroat (*O. clarki*) trout. In these transgenic lines, we have examined the growth-promoting effects and phenotypic consequences of chinook salmon GH expression by the ocean pout (*Macrozoarces americanus*) antifreeze protein promoter construct. This gene construct (opAFPGHc) has been used previously by Du et al. (1992), the first to report the production of dramatically growth-stimulated transgenic Atlantic salmon (*Salmo salar*).

Materials and methods

Experimental animals

Coho salmon eggs and milt were collected from spawning individuals during December through March of 1990, 1991, and 1992 at the Chehalis River hatchery in southwestern British Columbia. This is a late maturing strain that normally spawns in February. Smaller experiments were performed on several other salmonid species: cutthroat trout were collected from the Chehalis River in April 1992, Chinook salmon were collected from the Big Qualicum hatchery on Vancouver Island during November 1990, and wild rainbow trout were collected at the Pennask lake facility in south-central British Columbia during May 1992. Gametes were stored under O_2 at 4°C until use, for a maximum of 4 days postcollection. Microinjected embryos were maintained in Heath trays in a hatchery and transferred to 200-L aquaria supplied with 10 ± 1°C well water for the first 6 months of development. Subsequently, fish were reared to maturity in 2.4-m-diameter circular tanks. All rearing occurred indoors under a simulated natural photoperiod. All eggs and fish were reared in a secure hatchery and aquarium facility equipped with multiple containment screen systems designed to prevent the escape of genetically modified organisms to the natural environment.

Microinjection

To allow introduction of foreign DNA into the salmon eggs, a microinjection procedure for use with Pacific salmon eggs has been developed. Microinjection of large numbers of coho salmon eggs was found to be most efficient when eggs were fertilized in a buffered saline solution (Ginsburg 1963) and stored on ice until required. Under these conditions, fertilization and egg activation are separated, and no effect on viability was observed after storage in ice-cold Ginsburg's saline for several hours. Arresting egg activation in saline improves the visualization of the germinal disk, and slows the hardening of the chorion to allow penetration of the microinjection needle without breakage. Microinjection needles (5–10 μm outside diameter) were inserted through the chorion and vitelline membranes into the centre of the germinal disk region and approximately 1–2 nL of *Bam*HI-linearized opAFPGHc DNA solution (containing 100 μg/mL DNA in 1mM Tris, 0.1mM EDTA, 0.5% phenol red, pH 7.2) was introduced using a nitrogen-gas driven injection system (Eppendorf, model 5242). The needle was quickly withdrawn and the egg transferred to ice-cold well water. The construct opAFPGHc has been described previously (Du et al. 1992).

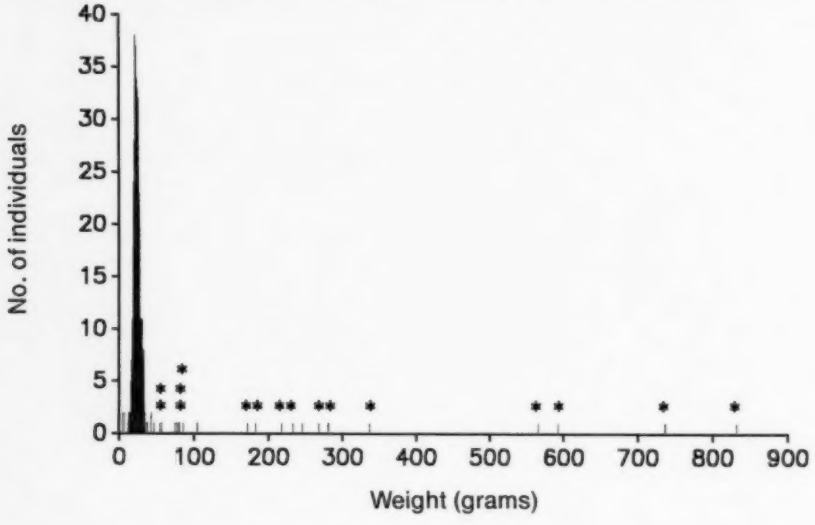
Polymerase chain reaction and Southern blot analysis

To test whether the microinjected fish were in fact transgenic for the new gene construct, DNA was prepared from a small tissue sample from the adipose fin and subjected to polymerase chain reaction (PCR) analysis using primers specific for the opAFPGHc gene construct. Fish were anaesthetized in 100 mg/L MS-222 and injected with a Passive Integrated Transponder (PIT) tag and their adipose fins removed. Crude DNA was prepared from adipose fins by digestion in 200 μL of K buffer (20 mM Tris, pH 8.3, 2.5 mM $MgCl_2$, 50 mM KCl, 0.5% Tween-20, 100 μg/mL proteinase K; Kawasaki 1990) for 60 min at 65°C, briefly vortexing after 30 min. The proteinase K and fin DNAs were denatured at 95°C for 10 min and the samples were centrifuged at 10 000 × *g* for 5 min and stored frozen for further analysis. Milt was also collected from mature males and DNA prepared as described (Devlin et al. 1991) to test for the presence of the gene construct in germ cells by PCR. PCR was conducted in 50 μL in Cetus buffer containing 10 mM Tris, pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$, 0.001% gelatin, 50 pmol of each appropriate primer, and 0.2 mM dNTPs. To ensure that amplifiable DNA was present in test samples, control sequences were amplified from the native growth hormone genes using primers GH-5 and GH-6 developed from sockeye salmon (*O. nerka*) GH genes (Devlin 1993). The presence of the introduced

Table 1. Viability of microinjected coho salmon eggs.

Group	No. injected	No. of eyed eggs	No. of alevins	Control hatch viability (%)	Viability of injected eggs relative to control (%)
Coho salmon (1990)	1508	1175	1108	85.0	86.5
Coho salmon (1991)	536	474	400	83.1	89.8
Rainbow trout (1992)	1439	967	403	36.2	77.5

Fig. 1. Frequency distribution of coho salmon derived from eggs microinjected with the opAFPGHc gene constuct. Weights were determined at 15 months of age. Individuals marked with an asterisk have retained the gene construct in blood or fin tissue.



opAFPGHc sequences were assessed using construct specific primers OP-A and OP-B described by Du et al. (1992). The sequences of the primers used were as follows: GH-5, 5′-GTCAGGATCCAGCCTGGATGACAATGACTC-3′; GH-6, 5′-GTCAGAATTCCTACAGAGTGCAGTTGGCCT-3′; OP-A, 5′-GTCAGAAGTCTCAGCTACAGC-3′; and OP-B, 5′-ATCTCAACAGTCTCCACAGGT-3′.

Southern blot analysis was performed to analyze the DNA structure of introduced DNA. DNA preparations and Southern blot analysis were performed as described by Devlin et al. (1991). Hybridizations were performed using a cDNA derived from the type-2 growth hormone gene (Devlin 1993) from sockeye salmon.

Results

The microinjection procedure resulted in good viability (88% of control values) of injected coho salmon eggs (Table 1). Seven months postfertilization, a large size class of fish was present in each injected group that was absent in the uninjected control tanks. During the fall, 8 months postfertilization, many of the large fish developed a characteristic silver colouration and lack of parr marks typical of coho salmon that have undergone the parr–smolt transformation. At 15 months of age, the majority of fish had a weight of approximately 26 g, but several individuals weighed up to 832 g, more than 30-fold greater than the group of smaller fish (Fig. 1). Figure 2A shows an intermediate and large transgenic coho salmon relative to a non-transgenic control.

At 13 months of age, 427 fish were examined for the presence of the new gene construct by PCR. Of 22 fish larger than two standard deviations above the mean, 17 were found to be positive in their fins, giving a frequency of transgenesis of 3.9% (Table 2). A similar frequency of gene retention was observed when this experiment was repeated the following year (Table 2, coho (1991)). Of the five fin-negative fish identified, one of these was found to be positive in blood indicating that integration of new DNA may be occurring after the first cell division and resulting in a mosaic distribution of the new gene insert in the tissues of some transgenic fish.

Transgenic fish had higher growth rates than their non-transgenic sibs, when measured both by weight (Fig. 3) and length, although the growth rate was elevated more at a younger age (5 months, 1991 brood) than with older

(15 months, 1990 brood) coho (Table 3). Throughout the experiment, transgenic salmon had a slightly lower condition factor than controls, indicating a disproportional stimulation of length relative to weight.

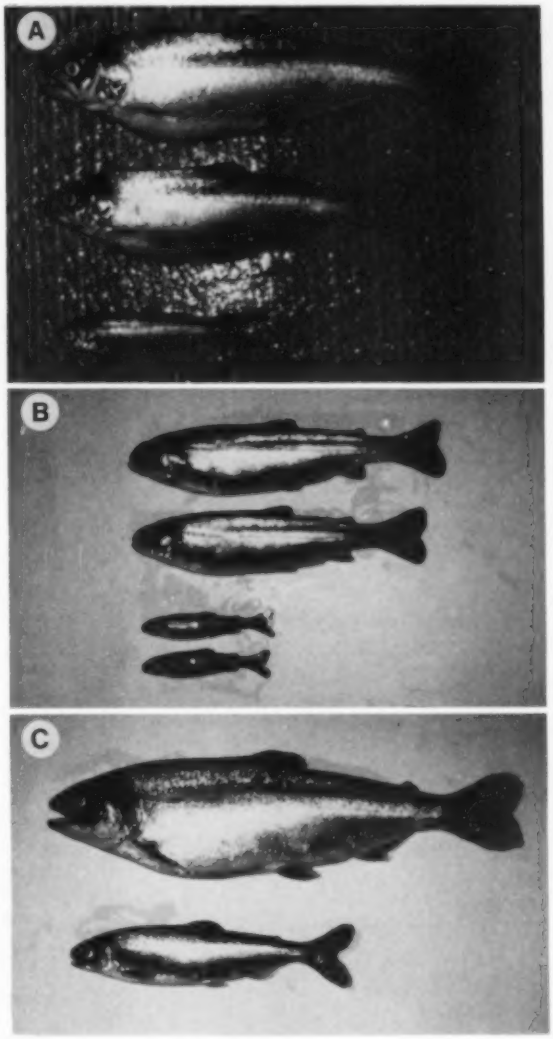
Three additional species of Pacific salmonids (chinook salmon, rainbow trout, and cutthroat trout) were also microinjected with the opAFPGHc construct. For rainbow trout, a weight distribution of transgenic individuals similar to that observed for coho salmon was obtained (Fig. 4), and growth data are shown in Table 3. However, the frequency of gene retention was approximately three-fold higher than that observed in coho (Table 2), and based on the proportion of large fish that were negative for the gene construct in their fin tissue (including the largest fish), it is possible that a high proportion of mosaicism is present in the rainbow trout P_1 population. Representative photographs of transgenic and control rainbow trout are shown in Fig. 2B. No large fish were obtained in a control tank of uninjected rainbow trout. Only a small experiment was conducted with chinook salmon, yielding two transgenic individuals. Figure 2C shows a transgenic (761 g) and a control (122 g) chinook salmon at age 19 months. Similarly, a small experiment with cutthroat trout produced several transgenic individuals that exhibited a similar growth enhancement (not shown). These additional experiments confirmed that the opAFPGHc gene construct has the potential to stimulate growth in several Pacific salmonid species.

The overall body morphology of most transgenic individuals did not appear to differ from nontransgenic individuals of the same size. However, some of the largest transgenic coho displayed a phenotypic syndrome consisting of head, fin, jaw, and opercular abnormalities arising from what superficially appeared to be excess cartilage and bone growth. In two cases, the cartilagenous tissue became overgrown such that the fish had difficulty eating and seeing. These fish had the best growth performance for the first 15 months postfertilization but subsequently showed poorer growth relative to other transgenic individuals, and ultimately died prior to maturation (Fig. 3).

At 2 years of age, five transgenic and several nontransgenic coho underwent sexual maturation in the late winter, the normal season for the strain employed. All maturing fish were males and milt samples were collected for DNA preparation from sperm cells. PCR analysis of sperm DNA showed that four of five transgenic fish had transmitted the new genetic information through their germ line into gametes (Fig. 5). The fish that appeared to be negative for the gene construct in sperm was a mosaic fish that possessed the opAFPGHc construct in blood but not fin tissue, and was apparently nontransgenic in testicular germ tissue as well.

To examine the genomic organization of the new genetic information in transgenic fish, Southern blot analysis was performed (Fig. 6) on DNA isolated from liver tissue of each transgenic male that transmitted the opAFPGHc construct to the next generation. *Bam*HI- or *Hin*dIII-digested genomic DNA from nontransgenic fish probed with a salmonid GH cDNA reveals only the presence of endogenous gene sequences corresponding to the coho salmon GH1 and GH2 loci. However, in three of four transgenic

Fig. 2. Photographs of transgenic and nontransgenic salmonids microinjected with opAFPGHc. (A) Coho salmon at 10 months of age. The top two fish are transgenic, and the bottom fish is a nontransgenic sibling of the same age. Note the loss of parr marks and silver colouration associated with the transgenic individuals. (B) Rainbow trout at 8 months of age. The top two fish are transgenic, and the bottom two are nontransgenic siblings. (C) Chinook salmon at 19 months of age. Top fish is transgenic and the bottom fish is a nontransgenic control. The lengths of the top fish in panels A, B, and C are 27.5, 25.8, and 35.6 cm, respectively.

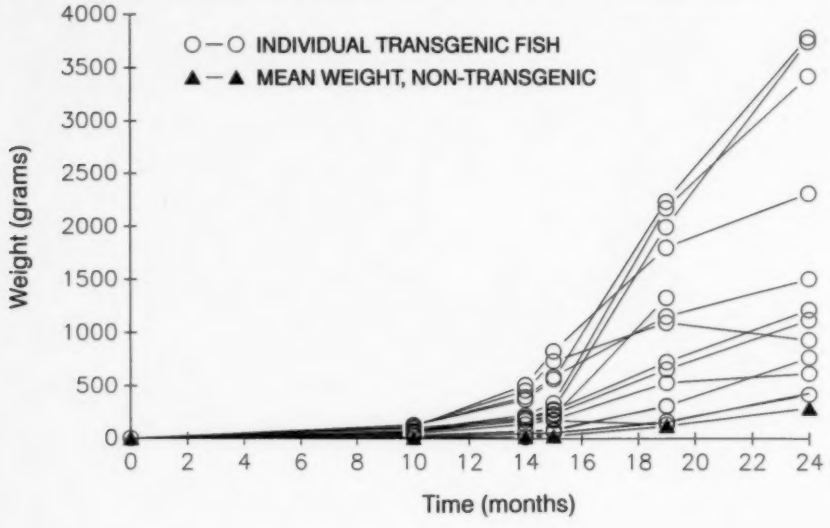


individuals, additional bands can be observed, indicating that the opAFPGHc sequences have been acquired. One fish (transgenic fish 3) shows no evidence of new gene sequences in liver DNA, but this fish was positive in sperm cells and fin tissue indicating a mosaic distribution of the

Table 2. Gene retention frequency in fin clips from P_1 fish developed from eggs microinjected with linear opAFPGHc DNA.

Group	No. tested by PCR	No. positive in fins	Gene retention (%)
Coho salmon (1990)	427	17	3.98
Coho salmon (1991)	191	9	4.71
Rainbow trout (1992)	131	16	13.74

Fig. 3. Growth curve of microinjected coho salmon over 2 years. Open circles represent individual weights of fish that retained the gene construct in blood or fin tissue. The closed triangle represents the average weight of over 400 nontransgenic individuals.



gene construct. Southern blots of undigested genomic DNA probed with a fragment of the ocean pout AFP promoter (not naturally present in the salmon genome) showed that homologous sequences were present in high molecular weight DNA of transgenic fish (not shown).

The intensity of the internal 2.2-kb *Hin*dIII fragment derived from opAFPGHc (migrating slightly above the endogenous 2.1-kb fragment) provides an estimate of the copy number of the construct in the liver tissue examined (Fig. 6). Relative to a control lane containing *Hin*dIII-digested opAFPGHc plasmid DNA equivalent to one copy per genome, average copy numbers of approximately 1, 10, and 0.3 were observed in the liver tissue extracted for transgenic fish 1, 2, and 4, respectively, although without knowing the degree of mosaicism it is not possible to precisely determine the number of copies per genome in those cells that are transgenic.

In *Bam*HI-digests of genomic DNA from transgenic fish, a band corresponding to the size of the injected opAFPGHc DNA (a 4.2-kb *Bam*HI fragment) can be seen, indicating that ends of the fragment were maintained during the integration event. This pattern is consistent with the presence of multiple copies of opAFPGHc fragments at a single site, perhaps arising from intermolecular ligation or replication occurring before integration occurred. *Bam*HI fragments larger than 4.2 kb indicate insertion sites that have not maintained the integrity of construct ends and arise from digestion in adjacent genomic junction fragments. The transgenic fish with the highest overall opAFPGHc copy number (see *Hin*dIII digest, transgenic fish 2) has only a small proportion of copies located together in the same chromosomal locus based on the *Bam*HI-digestion pattern. In contrast, transgenic fish 1 has most copies located adjacent to one another, and transgenic fish 4 (without a 4.2-kb band visible) has no more than two. These Southern blot analyses indicate that the injected DNA has integrated into the genome of the salmon at one or more locations and that multiple copies of the transgene are found at single insertion sites.

Discussion

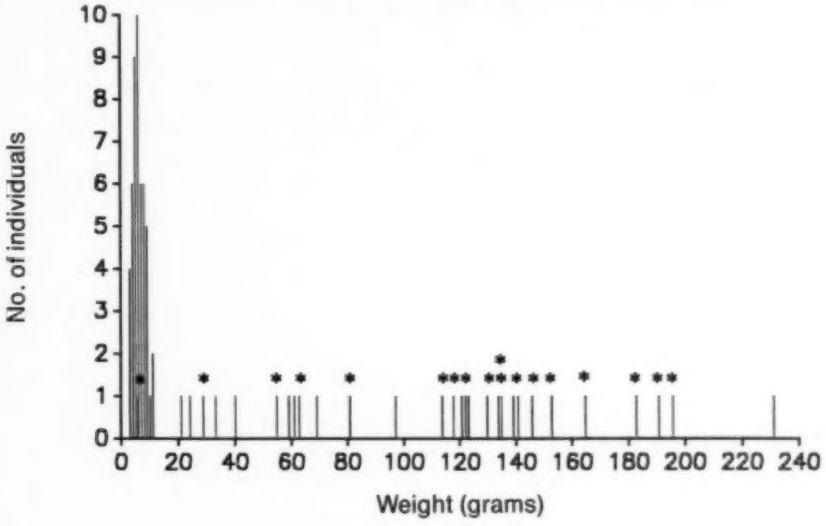
A variety of studies have developed successful methods for the introduction and expression of foreign DNA in fish (see Fletcher and Davies 1991 for review). We find that microinjection of the blastodisc region of eggs maintained in isotonic saline to prevent activation and chorion hardening (Ginsburg 1963) provides an efficient method for

Table 3. Growth performance of transgenic and control coho salmon and rainbow trout.

Group	Age (months)	Genotype	Weight (g)	Length (cm)	Condition factor	Growth rate* (weight)	Growth Rate* (length)	*N*
Coho salmon (1990)	15	Nontransgenic	26.1±1.7	12.9±0.1	9.0±0.3	1.82±0.03	0.36±0.04	370
		Transgenic	278.2±61.3	27.1±1.9	8.0±0.2	2.14±0.24	0.39±0.03	15
Coho salmon (1991)	5	Nontransgenic	3.9±0.4	6.6±0.2	11.0±0.2	1.03±0.26	0.34±0.07	25
		Transgenic	14.0±1.1	10.8±0.3	9.0±0.2	3.79±0.37	1.26±0.07	6
Rainbow trout (1992)	10	Non-transgenic	37.9±9.4	12.6±1.1	7.7±0.3	1.44±0.11	0.39±0.02	29
		Transgenic	119.5±12.4	21.6±12.4	7.8±0.2	1.64±0.16	0.42±0.03	18

Notes: Values are expressed as mean ± SE.
*Relative growth rate expressed in percent per day over 148 d for coho (1990), 17 d for coho (1991), and 50 d for rainbow trout (1992).

Fig. 4. Frequency distribution of rainbow trout derived from eggs microinjected with the opAFPGHc gene constuct. Weights were determined at 10 months of age. Individuals marked with an asterisk have retained the gene construct in blood or fin tissue.



producing transgenic Pacific salmonids. DNA is retained in P_1 individuals at a frequency of approximately 5%, with variable copy number and mosaic tissue distribution. These results are comparable with other transgenic studies with salmonids that have demonstrated long-term retention of foreign DNA (Chourrout et al. 1986; Fletcher et al. 1988; Guyomard et al. 1989; Penman et al. 1990, 1991; Yoshizaki et al. 1991; Du et al. 1992; Tewari et al. 1992; Devlin et al. 1994). We have observed transmission of the transgene to milt in 80% of maturing fish, indicating that germline transformation also occurs. Germline transmission of transgenic inserts in salmonids has also been observed in rainbow trout (Guyomard et al. 1989; Penman et al. 1991; Tewari et al. 1992) and Atlantic salmon (Shears et al. 1991), as well as in several nonsalmonid species (Stuart et al. 1988; Dunham et al. 1992; Lu et al. 1992; Chen et al. 1993).

The opAFPGHc construct used in the present experiments has a dramatic affect on the growth performance of transgenic individuals of several salmonid species. Du et al. (1992) reported an average fivefold stimulation in size of Atlantic salmon transgenic for this construct, with some fish as much as 13-fold larger. Our experiments with Pacific salmon have confirmed the potency of this construct, demonstrating an average size increase of more than 10-fold after 15 months of growth, with some individuals more than 30-fold larger than controls. We have shown that four species of Pacific salmonids (coho salmon, chinook salmon, rainbow trout, and cutthroat trout) are capable of significant increases in growth. A range of growth stimulations are observed among P_1 individuals, presumably arising from several factors including construct copy number, chromosomal site of integration, and degree of mosaicism. The growth stimulatory effects seen in this study and Du et al.

Fig. 5. Polymerase chain reaction analysis of DNA derived from the sperm of five somatically transgenic fish. The primers used were OP-A and OP-B, which are specific to the opAFPGHc gene construct. Lanes M, marker; lane +, positive control; lane −, no template control; lanes 1–5, sperm DNA from five individual transgenic fish.

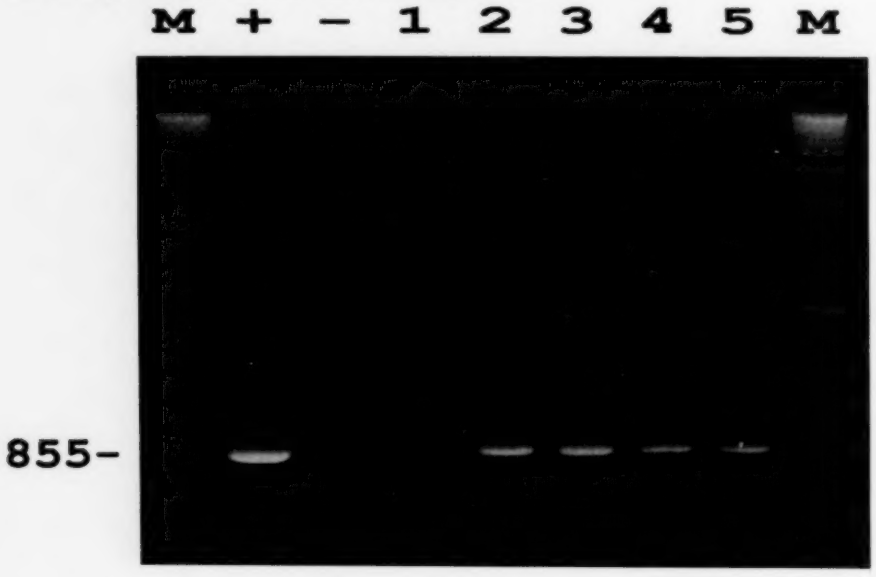
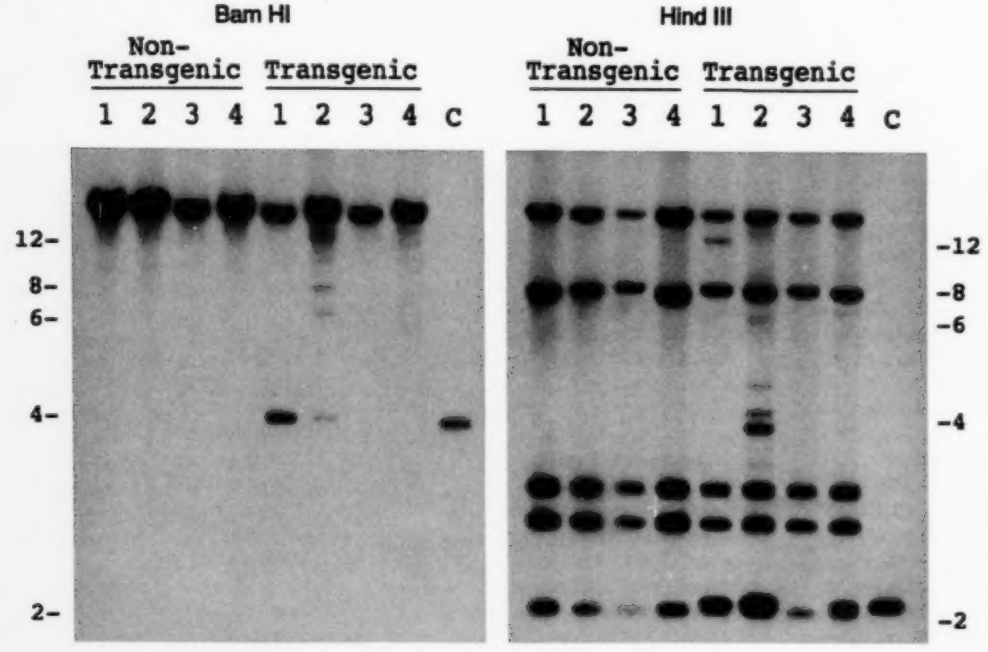


Fig. 6. Southern blot analysis of genomic DNAs (5 μg/lane) derived from liver tissue of four nontransgenic and four transgenic individuals. DNAs were digested either with *Bam*HI (left panel) or *Hin*dIII (right panel), and were probed with GH cDNA sequences. The lane marked C in each panel contains control opAFPGHc plasmid DNA digested with the indicated enzyme, and present at the equivalent of one copy per genome for 5 μg of genomic DNA. Molecular weight standards in kilobases are shown on each side.



(1992) with opAFPGHc are comparable with the 11-fold effect observed by Devlin et al. (1994) using a gene construct composed of the sockeye salmon metallothionein-B promoter fused to the type-1 growth hormone gene from the same species. It is currently unknown whether the dramatic growth effect seen in these experiments is due to the gene constructs employed or to an inherent capacity of salmonids for growth enhancement relative to other species.

The phenotypic alterations seen in this study are not limited to growth. Transgenic individuals undergo precocious smoltification, losing their parr marks and taking on the silver colouration typical of sea-running salmonids. These results are consistent with previous research showing an important role of endogenous GH in smoltification (Sweeting et al. 1985) and the ability of exogenous GH to promote seawater adaptiveness (Bolton et al. 1987). Coho salmon that have been induced to smolt by photoperiod manipulation show marked improvements in growth performance relative to nonsmolted controls (Clarke et al. 1989). Thus, it is possible that the dramatic growth stimulation observed in our experiments arises both by the direct actions of GH overexpression and by the indirect physiological effects of growth stimulation occurring through the smoltification process. The exact mechanism of growth stimulation and effects on smoltification in these transgenic fish will require a detailed evaluation of GH and IGF, and their receptors. Interestingly, transgenic fish which matured early as 2-year olds maintained the normal seasonal timing typical of their strain of origin. This suggests that, although the elevated growth of transgenics can accelerate maturation by annual increments, it does not appear to influence the response to cues that control the seasonal time of maturation.

Low levels of abnormalities were observed in fish transgenic for GH gene constructs in channel catfish (*Ictalurus punctatus*) (Dunham et al. 1992) but not in carp (*Cyprinus carpio*) (Chen et al. 1993). Morphological abnormalities were also induced in several of the transgenic fish produced in our experiments. These physical differences appeared to arise from an overproduction of cartilage, primarily in the cranial, jaw, and opercular regions of the head. Such a syndrome appears to be analogous to acromegaly in humans, arising from an overproduction of bone and cartilage because of excessive levels of GH production. It is also possible that elevated levels of GH and (or) IGF are responsible for these abnormalities in our transgenic salmon. It is known that IGF protein can stimulate cartilage growth in vitro in fish (Duan and Hirano 1990). It is important to note that not all transgenic fish display this abnormal phenotype and that the severity of the syndrome appears to be correlated with initial growth rate. Most transgenic individuals appear completely normal, but those fish that are initially stimulated to the greatest extent appear to have difficulty eating and soon fall behind in growth performance. In this respect, transgenic strains with an increased growth rate and normal morphology are to some degree self-selecting. These results suggest that detrimental stimulation of growth in transgenic salmonids can occur and that optimal long-term stimulation may be best achieved in transgenic individuals that do not show the highest initial growth rates.

The results of this and other studies (Du et al. 1992; Devlin et al. 1994) have shown a clear capacity for the growth of salmonids to be manipulated by transgenic technologies. Increases in growth performance of the magnitude observed in these experiments may have significant potential for increasing the efficiency of aquaculture production by reducing production times and improving feed conversion efficiencies. However, to be useful in the future, it will be necessary to evaluate the performance and quality of these transgenic organisms carefully in controlled large-scale trials. Considering the possibility of accidental escapes of cultured transgenic salmon, it is important that appropriate physical and biological containment procedures (Devlin and Donaldson 1992) be developed to minimize any possible ecological impacts.

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References

Bolton, J.P., N.L., Collie, H. Kawauchi, and T. Hirano. 1987. Osmoregulatory actions of growth hormone in rainbow trout (*Salmo gairdneri*). J. Endocrinol. 112: 63–68.

Chen, T., and D.A. Powers. 1990. Transgenic fish. Trends in Biotechnol. **8**: 209–215.

Chen, T.T., K. Kight, C.M. Lin, D.A. Powers, M. Hayat, N. Chatakondi, A.C. Ramboux, P.L. Duncan, and R.A. Dunham. 1993. Expression and inheritance of RSVLTR-rtGH1 complementary DNA in the transgenic common carp, *Cyprinus carpio*. Mar. Mol. Biol. Biotechnol. 2: 88–95.

Chourrout, D., R. Guyomard, and L.-M. Houdebine. 1986. High efficiency gene transfer in rainbow trout (*Salmo gairdneri* Rich.) by microinjection into egg cytoplasm. Aquaculture, 51: 143–150.

Clarke, W.C., J.E. Shelbourne, T. Ogasawara, and T. Hirano. 1989. Effect of initial daylength on growth, seawater adaptability and plasma growth hormone levels in underyearling coho, chinook and chum salmon. Aquaculture, 82: 51–62.

Devlin, R.H. 1993. Sequence of sockeye salmon type 1 and 2 growth hormone genes and the relationship of rainbow trout with Atlantic and Pacific salmon. Can. J. Fish. Aquat. Sci. 50: 1738–1748.

Devlin, R.H., and E.M. Donaldson. 1992. Containment of genetically altered fish with emphasis on salmonids. pp. 229–265. *In* C. Hew and G. Fletcher [ed.] Transgenic fish. World Scientific Publishing Co., Singapore.

Devlin, R.H., B.K. McNeil, T.D.D. Groves, and E.M. Donaldson. 1991. Isolation of Y-chromosomal DNA probe capable of determining genetic sex in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 48: 1606–1612.

Devlin, R.H., T.Y. Yesaki, C.A. Biagi, E.M. Donaldson, P. Swanson, and W.-K. Chan. 1994. Extraordinary salmon growth. Nature (London), 371: 209–210.

Du, S.J., Z. Gong, G.L. Fletcher, M.A. Shears, M.J. King, D.R. Idler, and C.L. Hew. 1992. Growth enhancement in transgenic Atlantic salmon by the use of an "all fish"

chimeric growth hormone gene construct. Bio/Technology, 10: 176–180.

Duan, C., and T. Hirano. 1990. Stimulation of ^{35}S-sulfate uptake by mammalian insulin-like growth factors I and II in cultured cartilages of the Japanese eel, *Anguilla japonica*. J. Exp. Zool. 256: 347–350.

Dunham, R.A., A.C. Ramboux, P.L. Duncan, and M. Hayat. 1992. Transfer, expression and inheritance of salmonid growth hormone in channel catfish, *Ictalurus punctatus*, and effects on performance traits. Mol. Mar. Biol. Biotechnol. 1: 380–389.

Enikolopov, G.N., A.O. Benyumov, A. Barmintsev, I.A. Zelenina, L.A. Sleptsova, Y.K. Doronin, V.A. Golichenkov, M.A. Grashchuk, G.P. Academician Georgiev, P.M. Rubtsov, K.G. Skryabin, and A.A. Academician Baev. 1989. Advanced growth of transgenic fish containing human somatotropin gene. Dokl. Akad. Nauk SSSR, 301: 724–727.

Fletcher, G., and P.L. Davies. 1991. Transgenic fish for aquaculture. Genet. Eng. 13. pp. 331–369.

Fletcher, G.L., M.A. Shears, M.J. King, P.L. Davies, and C.L. Hew. 1988. Evidence for antifreeze protein gene transfer in Atlantic salmon. Can. J. Fish. Aquat. Sci. 45: 352–357.

Ginsburg, A.S. 1963. Sperm–egg association and its relationship to the activation of the egg in salmonid fishes. J. Embryol. Exp. Morphol. 2: 13–33.

Gross, M.L., J.F. Schneider, N. Moav, B. Moav, C. Alvarez, S.H. Myster, Z. Liu, E.M. Hallerman, P.B. Hackett, K.S. Guise, A.J. Faras, and A.R. Kapuscinski. 1992. Molecular analysis and growth evaluation of northern pike (*Esox lucius*) microinjected with growth hormone genes. Aquaculture, **103**: 253–273.

Guyomard, R., D. Chourrout, C. Leroux, L.-M. Houdebine, and F. Pourrain. 1989. Integration and germ line transmission of foreign genes microinjected into fertilized trout eggs. Biochimie, 71: 857–863.

Houdebine, L.M., and D. Chourrout. 1991. Transgenesis in fish. Experientia, 47: 891–897.

Kawasaki, E.S. 1990. Sample preparation from blood, cells, and other fluids. pp. 146–152. *In* M.A. Innis, D.H. Gelfand, J.J. Sninsky, and T.J. White [ed.] PCR protocols. Academic Press, San Diego, Calif.

Lu, J.-K., T.T. Chen, C.L. Chrisman, O.M. Andrisini, and J.E. Dixon. 1992. Integration, expression and germ-line transmission of foreign growth hormone genes in medaka (*Oryzias latipes*). Mol. Mar. Biol. Biotechnol. 1: 366–375.

Maclean, N., and D. Penman. 1990. The application of gene manipulation to aquaculture. Aquaculture, 85: 1–20.

McLean, E., and E.M. Donaldson. 1993. The role of growth hormone in the growth of poikilotherms. pp. 43–71. *In* M.P. Schreibman, C.G. Scanes, and P.K.T. Pang [ed.] The endocrinology of growth, development and metabolism in vertebrates. Academic Press, San Diego, California.

Penman, D.J., A.J. Beeching, S.Penn, and N. Maclean. 1990. Factors affecting survival and integration following microinjection of novel DNA into rainbow trout eggs. Aquaculture, 85: 35–50.

Penman, D.J., A.J. Beeching, S. Penn, A. Rhaman, Z. Sulaiman, and N. Maclean. 1991. Patterns of transgene inheritance in rainbow trout (*Oncorhynchus mykiss*). Mol. Reprod. Dev. 30: 201–206.

Shears, M.A., G.L. Fletcher, C.L. Hew, S. Gauthier, and P.L. Davies. 1991. Transfer, expression and stable inheritance of antifreeze protein genes in Atlantic salmon (*Salmo salar*). Mar. Mol. Biol. Biotechnol. 1: 58–63.

Stuart, G.W., J.V. MacMurray, and M. Westerfield, M. 1988. Replication, integration and stable germ-line transmission of foreign sequences injected into early zebrafish embryos. Development (Cambridge, U.K.), 103: 403–412.

Sweeting, R.M., G.F. Wagner, and B.A. McKeown. 1985. Changes in plasma glucose, amino acid nitrogen and growth hormone during smoltification and seawater adaptation in coho salmon, *Oncorhynchus kisutch*. Aquaculture, 45: 185–197.

Tewari, R., C. Michard-Vanhee, E. Perrot, and D. Chourrout. 1992. Mendelian transmission, structure and expresssion of transgenes following their injection into the cytoplasm of trout eggs. Transgenic Res. 1: 250–260.

Yoshizaki, G., T. Oshiro, and F. Takashima. 1991. Introduction of carp α-globin gene into rainbow trout. Nippon Suisan Gakkaishi, 57: 819–824.

Zhang P., M. Hayat, C. Joyce, L.I. Gonzalez-Villasenor, C.M. Lin, R.A. Dunham, T.T. Chen, and D.A. Powers. 1990. Gene transfer, expression and inheritance of pRSV-rainbow trout-GHcDNA in the carp, *Cyprinus carpio* (Linnaeus). Mol. Reprod. Dev. 25: 3–13.

Zhu, Z. 1992. Generation of fast growing transgenic fish: methods and mechanisms. pp. 92–119. *In* C. Hew and G. Fletcher [ed.] Transgenic fish. World Scientific Publishing Co., Singapore.

Relation of grilse to salmon ratio to environmental changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland

S. Gudjonsson, S.M. Einarsson, Th. Antonsson, and G. Gudbergsson

Abstract: The grilse to salmon ratio of each smolt class of Atlantic salmon (*Salmo salar*) during the last three decades were examined using data from catch records and from direct counter data in several rivers in western and northern Iceland. The counter data show that the catch data in Icelandic rivers reflects the number of spawners entering the rivers. Both long- and short-term changes in the grilse to salmon ratio were seen. Climatic changes can be responsible for long term changes in sea age composition of Icelandic salmon stocks. Short-term changes in the ratio can be explained by changes in marine conditions that influence the survival of salmon during their second year at sea.

Résumé : Nous avons examiné le rapport madeleineaux à saumons de chaque classe de smolts du saumon de l'Atlantique (*Salmo salar*) pendant les trois dernières décennies, en nous servant de données provenant des registres de captures et à partir de dénombrements directs effectués dans plusieurs cours d'eau de l'ouest et du nord de l'Islande. Les dénombrements montrent que les données sur les captures dans les cours d'eau islandais correspondent au nombre de géniteurs en montaison. Nous avons observé des changements à long terme et à court terme dans le rapport madeleineaux à saumons. Les changements climatiques peuvent être responsables des variations à long terme de la composition des stocks de saumons islandais quant à la durée de leur vie en mer. Les changements à court terme du rapport peuvent s'expliquer par des changements de conditions océaniques qui influent sur la survie des saumons pendant leur deuxième année en mer.
[Traduit par la Rédaction]

Introduction

Catches of Atlantic salmon (*Salmo salar*) from Icelandic rivers are known to vary severalfold between years (Scarnecchia 1984*a*). This variation is more pronounced in northern and eastern rivers where up to 20-fold annual variation in catches can be observed (Gudbergsson and Arnason 1993). The sources of this variation can be attributed to fluctuations in the natural smolt production in the river systems, variable survival of smolts in the marine phase of the salmon life cycle, and how accurately angling effort reflects the actual numbers of spawners entering the rivers.

Recent studies from Newfoundland (Chadwick 1988; Reddin 1988) have indicated that survival during the marine phase of the salmon is four times more variable there than the survival in freshwater. Similar results from Iceland showing greater variability in the marine phase are available for the rivers Ellidaar and Vesturdalsa (Antonsson and Gudjonsson 1993*a*, 1993*b*). Studies on catch statistics in Icelandic rivers have provided evidence that the rod fishery reflects the actual abundance of spawning runs (Scarnecchia 1984*a*, 1984*b*; Mundy et al. 1978). The operation of a fish trap in River Blanda, northern Iceland, have also provided evidence for the relation between catches and the size of the spawning runs.

Oceanic conditions along the coasts of Iceland vary markedly between years; in the sea north and east of Iceland, conditions fluctuate more than in the sea south and west of Iceland, as do primary production and abundance of zooplankton (Astthorsson et al. 1983).

Oceanic conditions off Icelandic coasts have been linked to several aspects of the marine life history of salmon. Scarnecchia (1984*a*) and Scarnecchia et al. (1989*a*, 1989*b*, 1991) correlated variation in climate, weather, and river hydrology to changes in primary production and salmon catches in Iceland and found significant relationships between mean June–July sea temperatures and the catch of grilse the following year. Furthermore, significant relationships between grilse catch in one year and the salmon catch in the following year have been found for numerous Icelandic rivers (Kristjansson 1982; Scarnecchia 1984*b*; Scarnecchia et al. 1989*c*). Martin and Mitchell (1985) have demonstrated that long-term changes in grilse to salmon

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ratios in Scottish rivers are associated with changes in sea temperatures. Increased temperatures resulted in increased numbers of multi-sea-winter salmon in the River Dee.

Accurate catch statistics for Icelandic rivers, relatively constant fishing effort in the rod fishery, and a ban on any sea fishery inside Iceland's 200-mile (1 mile = 1.6 km) exclusive Economic Zone all contribute to creating suitable conditions for investigating fluctuations in the salmon catches and their causes. The aim of this paper was to investigate both short- and long-term fluctuation in the grilse to salmon ratio and the influence of year-to-year changes in sea temperatures on the ratio.

Materials and methods

Relations between the grilse and two-sea-winter salmon ratio and ocean conditions were investigated for seven Icelandic rivers located in the western, northern, and northeastern parts of the country. Catch statistics from Icelandic rivers consists of date and location of capture, weight, and sex of fish captured (Scarnecchia 1983). Further description of the Icelandic sport fishery is given by Gudjonsson (1978) and Scarnecchia (1989). Long series of catch statistics (up to 50 years) are available for some rivers although in the earlier years the records are not as accurate. For three widely separated rivers with good long term catch statistics, Hofsa, Vididalsa and Nordura (Fig. 1), these records where used to calculate the number of grilse and salmon caught from each smolt cohort from 1960 to 1990. To do so the annual catch was divided into males and females and both sexes divided into grilse (1 year at sea) and salmon (2 years at sea) using weight-frequency distributions. Generally, males over 4 kg and females over 3.5 kg were considered as salmon. Scale readings from part of the catch aided this work in several cases. Three-sea-winter salmon (over 8–9 kg) were scarce or absent depending on river. Male and female grilse were then combined as well as salmon of both sexes. The grilse catch in the year n was added to the salmon catch in the year $n + 1$ and these two components represented the catch from the smolt cohort in the year $n - 1$. Three-sea-winter fish were omitted, because they constituted very small fraction of the total run.

A fourth river, Blanda, has had an operational fish trap since 1982, where all fish migrating upstream are measured and scale samples taken from part of the run. Since 1982 the actual number of grilse and salmon in the spawning run has been known. Therefore, information on the returns from the 1981–1990 smolt cohorts is used and compared with the catch data for the three rivers already mentioned, as well as three other rivers, Thvera, Laxa i Adaldal, and Sela (Fig. 1), where the catch data was analyzed as described earlier for the smolt cohorts 1981–1990.

The salmon ratio was calculated as the number of salmon in one smolt cohort divided by the number of grilse and salmon from the same smolt cohort:

$$[1]\quad \text{Salmon ratio} = \frac{\text{No. of salmon in smolt cohort } n}{(\text{No. of grilse} + \text{No. of salmon}) \text{ for the smolt cohort } n}$$

Oceanic temperature measurements (0–200 m depth) in the spring (April–May) each year of a transect off Siglunes, northern Iceland, and Latrabjarg, Northwestern Iceland (Fig. 1) were obtained from the Marine Research Institute, Reykjavik (Anonymous 1992). Average temperatures were calculated using five stations on the Siglunes transect and seven stations on the Latrabjarg transect. In both instances the stations were the ones closest to Iceland. The mean temperature in the spring when the smolt were going to sea and the following year was calculated and used in all comparisons, because it was considered as being descriptive for the oceanic condition during the sea phase of the smolt cohorts.

When dealing with environmental factors and time series, adjacent data values can be highly correlated (Box and Jenkins 1976). Therefore, the data in this study were tested for autocorrelation by the use of SPSS statistical package (Norusis 1993). Some autocorrelation was found between the salmon catch data in one year and the catch 1 year later. That is not surprising because the salmon entering rivers in one year stayed at sea during the same time as the salmon that entered rivers 1 year earlier. Therefore, a model was tested for the relation of grilse and salmon from the same smolt cohort for the Nordura, Vididalsa, and Hofsa rivers, using multiple regression where salmon catch from the same cohort as well as salmon catch 1 year earlier were entered in the model. The salmon catch 1 year earlier did not improve the model. Therefore, linear regression methods were used to find the relation of grilse and salmon from the same smolt cohort for the Nordura, Vididalsa, and Hofsa rivers, then the deviation of each data point from the regression line (the residuals) was plotted.

Correlation coefficients were obtained for the relations between number of grilse and salmon in River Blanda and the corresponding number of grilse and salmon in the catch in the other rivers and the temperature at Siglunes and Latrabjarg. Furthermore, the correlation coefficients of the salmon ratio between rivers were calculated.

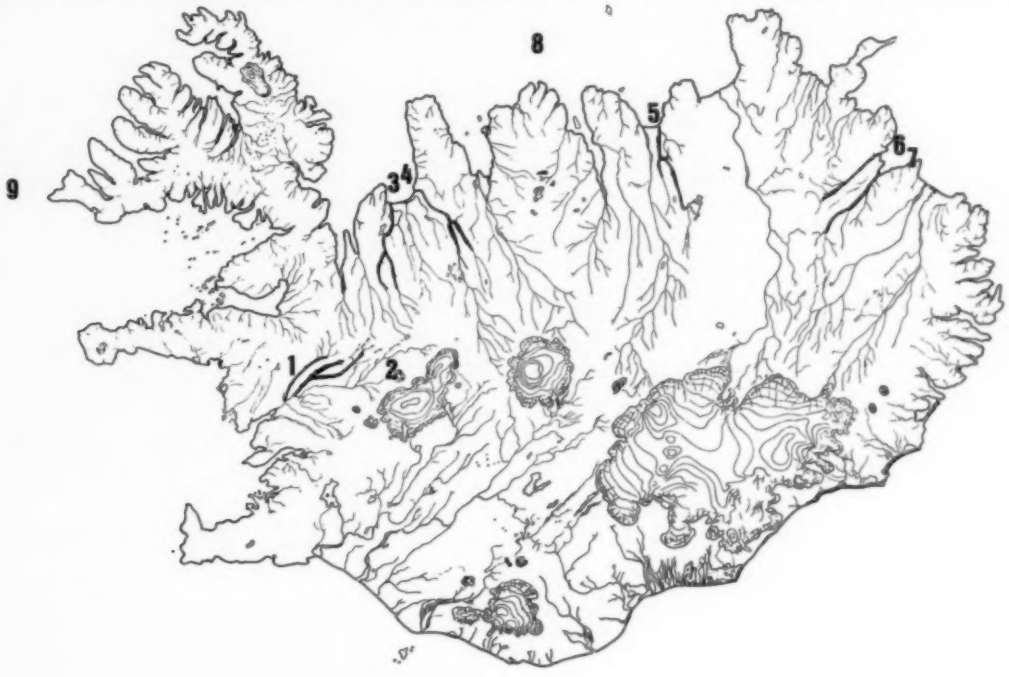
Results

For the smolt cohorts 1960–1990, the catches were most stable in River Nordura, western Iceland, intermediate in River Vididalsa, northwestern Iceland and most variable in River Hofsa, northeastern Iceland (Fig. 2). The grilse to salmon ratio fluctuated in these rivers during the time period (Fig. 3).

The relation between grilse (year n) and salmon (year $n + 1$) were highly significant in all three rivers (Fig. 4). The data points in some years deviated from the regression line and often in sequence so that points for some consecutive years were above the line and the points for the next period were below it (Fig. 5), indicating long-term periodic changes in the grilse to salmon ratio. In general, the ratio of salmon seemed to be lower in the colder years, but the mean temperatures at the Siglunes and Latrabjarg transects varied greatly during this period (Fig. 6). For the period 1970–1990 where data is available, the correlation coefficient of the two temperature transects was 0.68 ($p < 0.05$).

When actual numbers of grilse and salmon entering River Blanda were compared with the catch in the

Fig. 1. Location of salmon rivers and the Siglunes and Latrabjarg temperature transects: (1) Nordura; (2) Thvera; (3) Vididalsa; (4) Blanda; (5) Laxa i Adaldal; (6) Sela; (7) Hofsa; (8) Siglunes; (9) Latrabjarg.



neighbouring River Vididalsa, a similar fluctuation could be seen and this fluctuation was also seen in Laxa i Adaldal (Tables 1 and 2). This confirms that the catch statistics really reflect the size of the spawning runs. Rivers in western Iceland showed less fluctuation and those in northeastern Iceland showed greater fluctuation; in both cases, rivers fluctuated together (Fig. 7, Tables 1 and 2). When the grilse to salmon ratio was examined the same fluctuation was seen within the rivers in the same area but not as clearly between these three regions (Fig. 8). This was examined closer with the correlation between the number of grilse and salmon in the rivers (Tables 1 and 2). The temperature at Siglunes was significantly correlated to grilse number in most of the rivers, and the other rivers showed the same trend (Table 1). The temperature at the Latrabjarg transect was not correlated to the grilse number in any river (Table 1). When numbers of salmon were compared, rivers in northeastern and northern Iceland seemed to fluctuate together along with the temperature, but the rivers in western Iceland showed another trend and were even negatively correlated with the temperature at Siglunes but were not correlated with the temperature at Latrabjarg (Table 2). When the salmon ratio was examined, it can be seen that the rivers in northeastern Iceland were correlated among themselves, but were not correlated to any other rivers; in contrast the rivers in northern Iceland correlated with one another and, in most cases, with the rivers in western Iceland or showed the same trend (Table 3).

Large short term variations in the salmon ratio were observed (Fig. 8), where the ratio changed from 23 (minimum) to 72% (maximum) in River Blanda, which is the best data set for the period under examination (1981–1990).

Discussion

The data obtained from the operation of the fish trap in Blanda show that the catch reflect the number of spawners in Icelandic rivers. This evidence has long been needed.

It is well known that the salmon catch of Icelandic rivers varies from year to year depending on the oceanic conditions and that the variation in catch is greater in the rivers in northern Iceland than in western Iceland (Scarnecchia 1984*a*; Scarnecchia et al. 1989*a*, 1989*b*). Our study gave the same conclusion, and the fluctuations are greatest in the northeast. This can be better understood by looking at the mechanism of sea currents around Iceland. A branch from the warm Gulf Stream, the Irminger Current flows along the south coast of Iceland and goes clockwise around the island meeting the cold East Greenland and the Icelandic currents northwest and north of Iceland. It depends on the strength of these currents if this warm current extends to the sea north of Iceland. In some years it does not reach there, resulting in low temperature and salinity, little turbulent mixing, and failure or changes in primary production there (Stefansson 1961). These oceanographic changes affect the abundance of zooplankton (Astthorsson et al. 1983) and the growth and survival of

Fig. 2. Catch of grilse (solid bars) and salmon (open bars) from the smolt cohorts, the years 1960–1990.

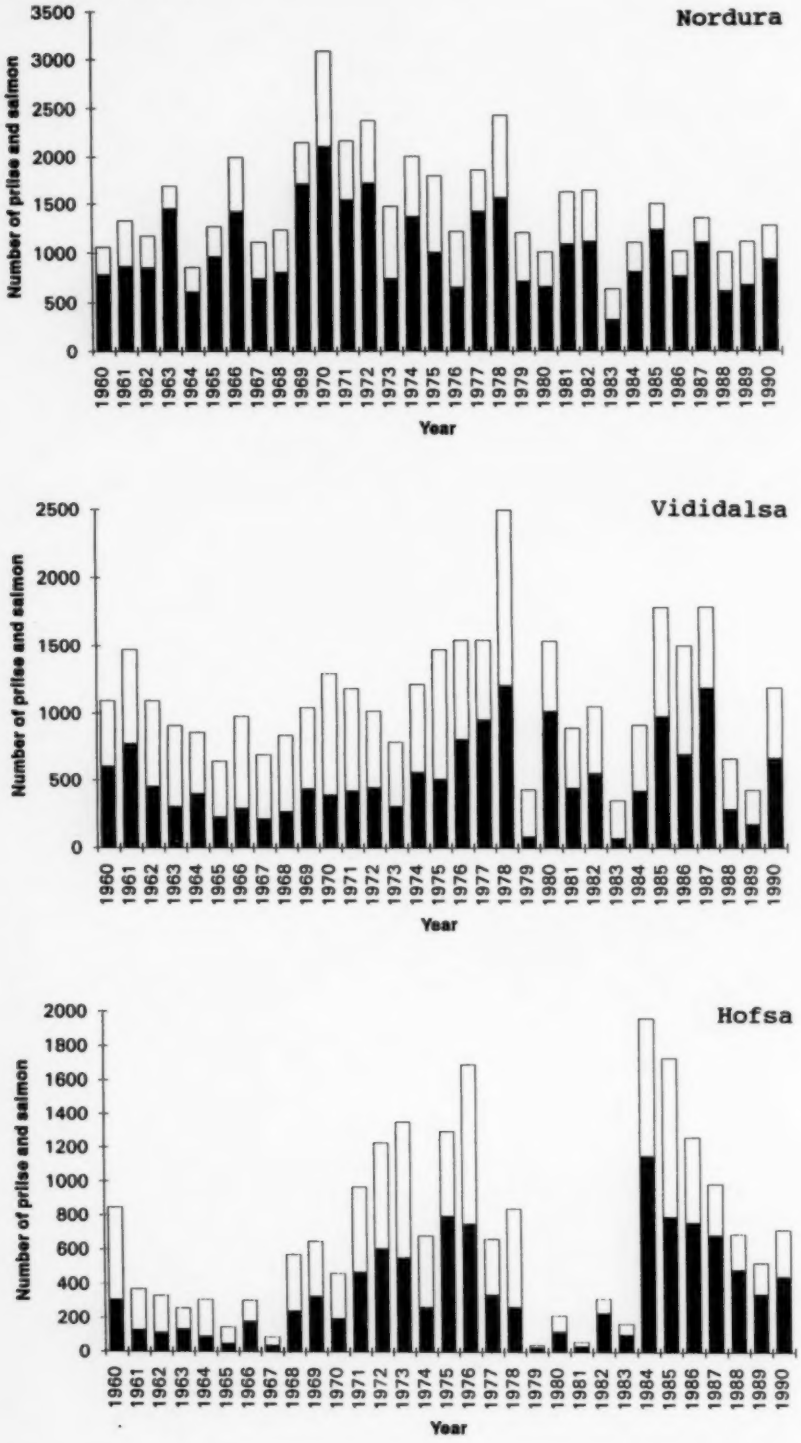


Fig. 3. The proportion of grilse (solid bars) and salmon (open bars) in the smolt cohorts for the years 1960–1990.

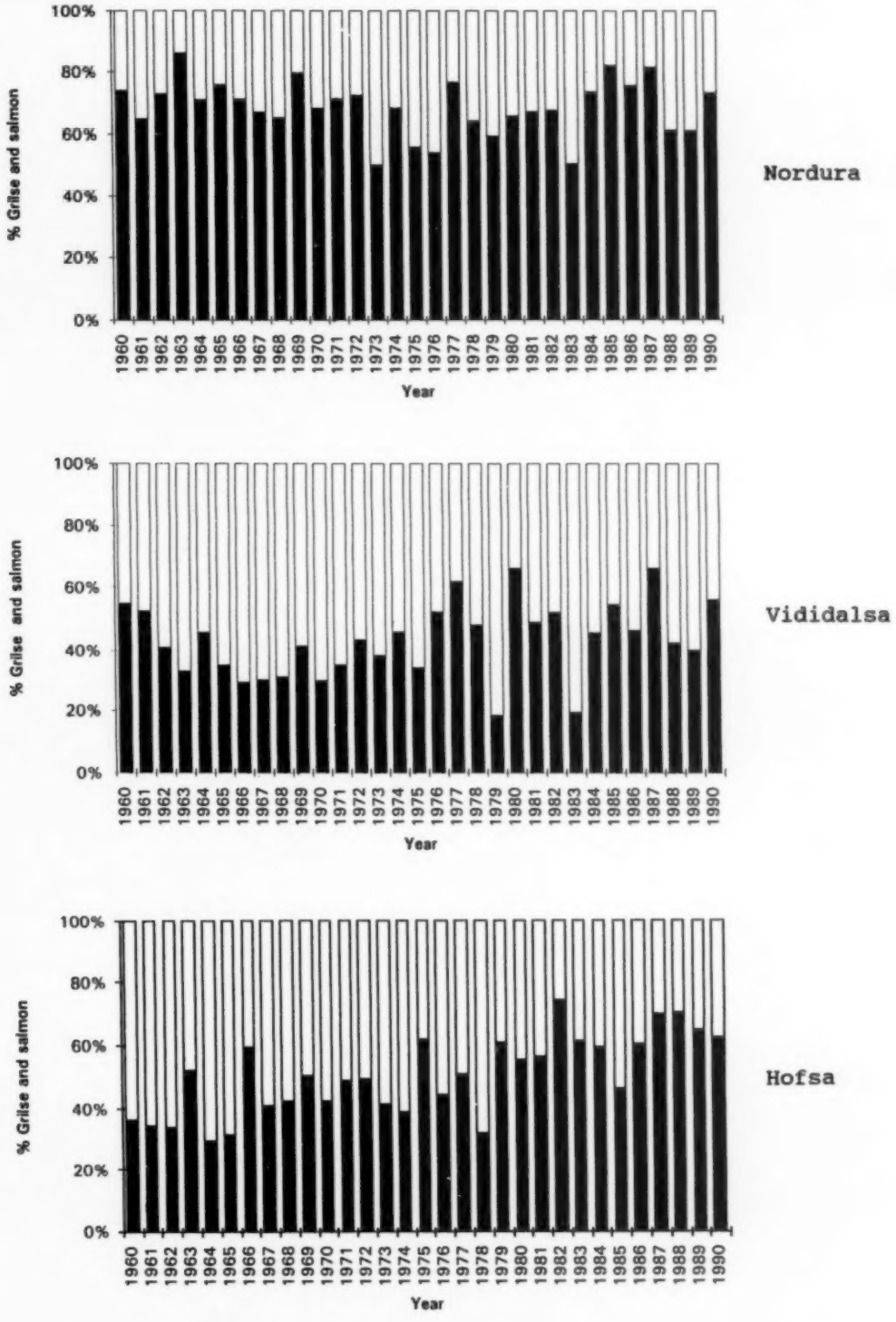


Fig. 4. The relation of grilse and salmon in river Nordura, Vididalsa, and Hofsa for the smolt cohorts 1960–1990. Linear equation for Nordura is $Y = 199.7 + 0.26X$, $R^2 = 0.29$, $P < 0.001$; for Vididalsa is $Y = 398.8 + 0.38X$, $R^2 = 0.32$, $P < 0.001$; for Hofsa is $Y = 81.5 + 0.75X$, $R^2 = 0.64$, $P \leq 0.001$ and where Y = no. of salmon and X = no. of grilse.

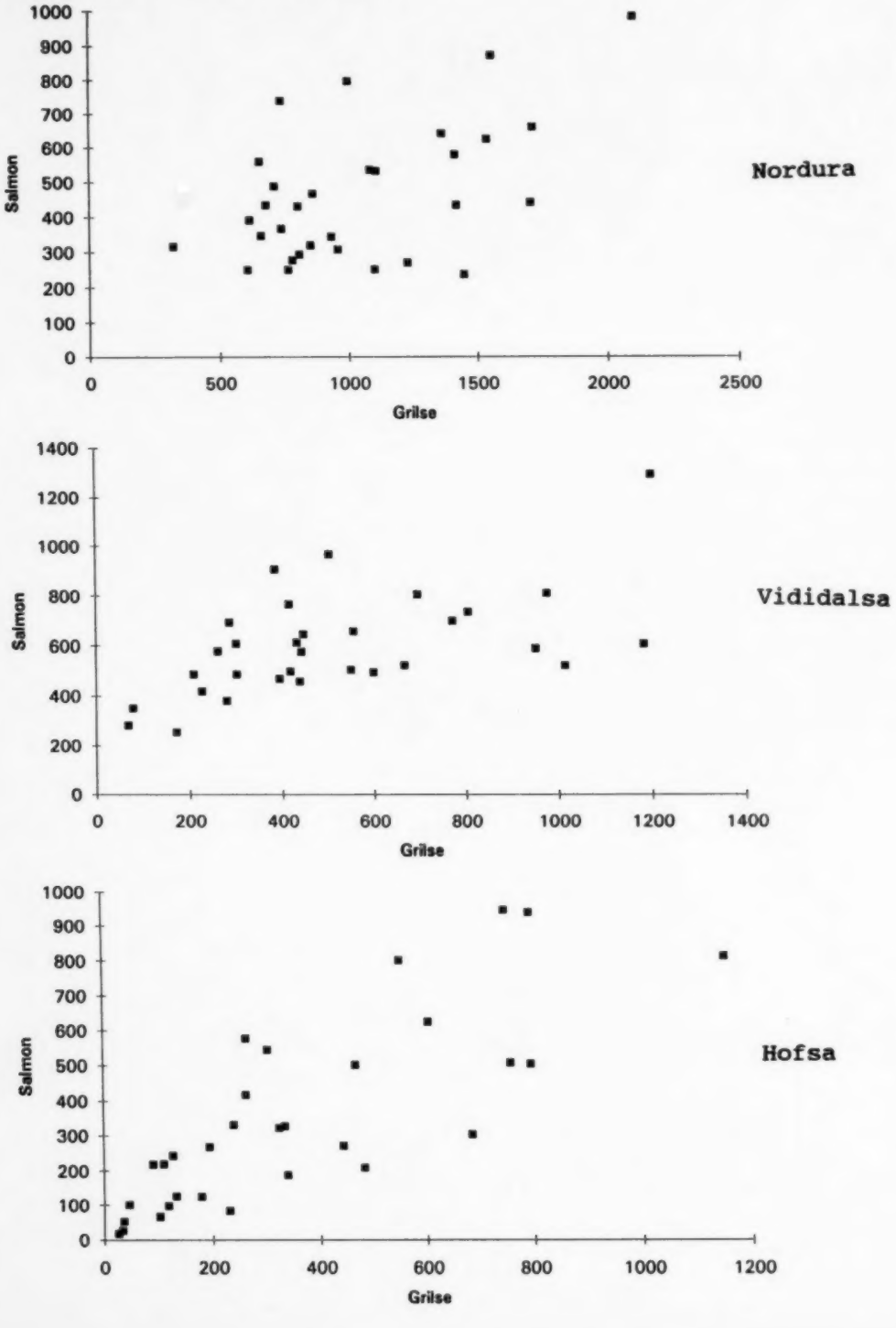


Fig. 5. Deviation of data points from the regression lines presented in Fig. 4.

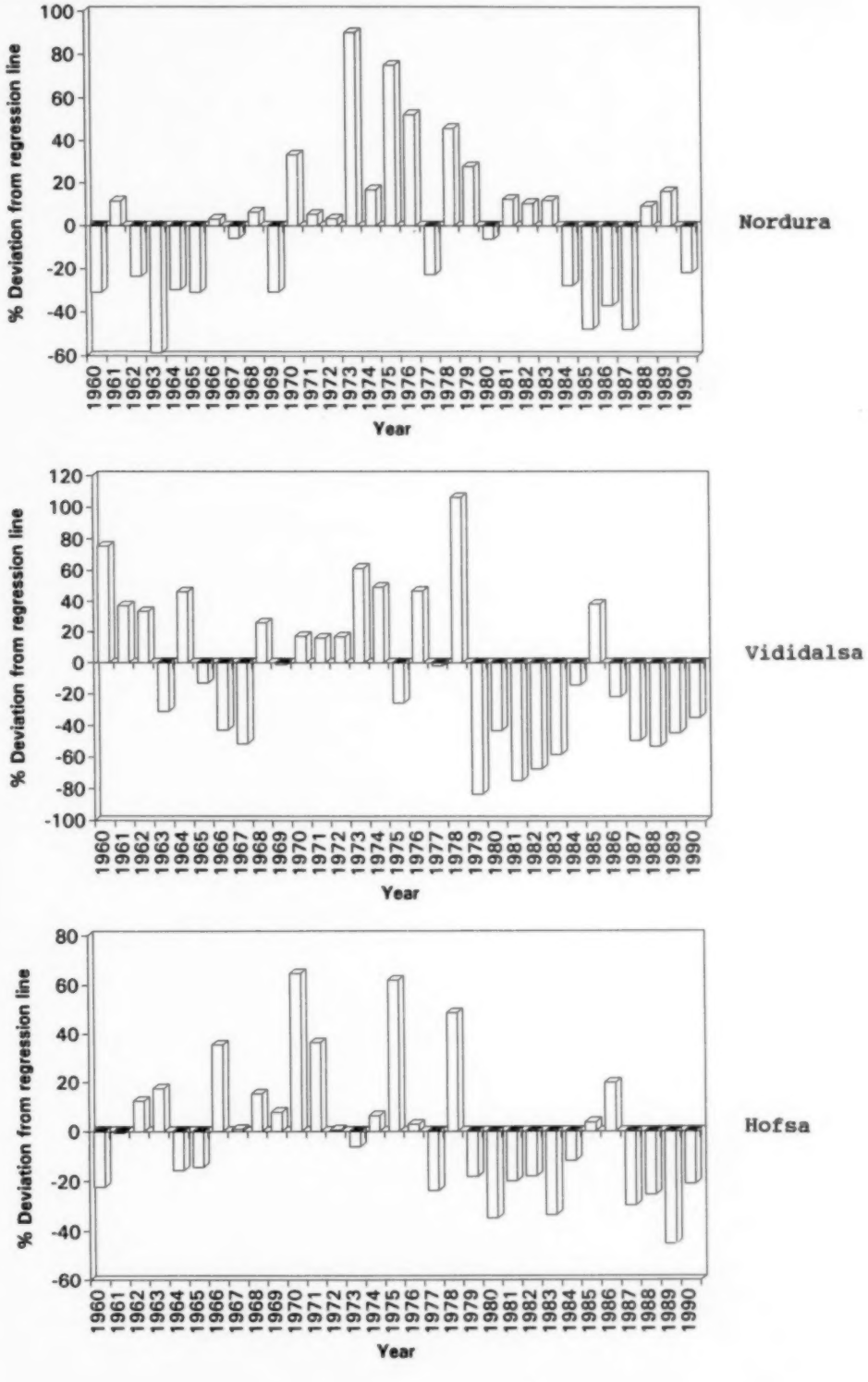


Fig. 6. Temperature at the Siglunes transect 1960–1990 and at the Latrabjarg transect 1970–1990.

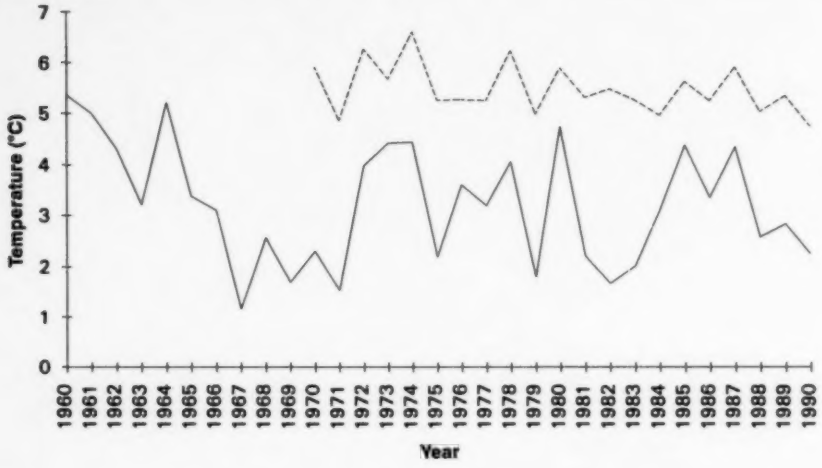


Table 1. Correlation coefficients of mean temperature at Siglunes and Latrabjarg, the grilse count in River Blanda and the grilse catch from six other rivers in Iceland for the smolt cohorts 1981–1990.

	Temperature at Latrabjarg	Temperature at Siglunes	Blanda	Vididalsa	Laxa i Adaldal	Sela	Hofa	Nordura	Thvera
Temperature at Latrabjarg									
Temperature at Siglunes	−0.37ns								
Blanda	−0.53ns	0.76*							
Vididalsa	−0.33ns	0.55ns	0.62*						
Laxa i Adaldal	−0.45ns	0.75*	0.66*	0.76*					
Sela	−0.33ns	0.88***	0.73*	0.67*	0.78**				
Hofsa	−0.37ns	0.86**	0.89***	0.46ns	0.66*	0.85**			
Nordura	−0.28ns	0.11ns	0.48ns	0.77**	0.55ns	0.30ns	0.19ns		
Thvera	−0.12ns	0.48ns	0.54ns	0.61ns	0.65*	0.51ns	0.39ns	0.72*	

Note: Level of significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant.

different fish species such as cod (*Gadus morhua*) and capelin (*Mallotus villosus*) (Malmberg 1986) as well as salmon (Scarnecchia 1984*a*, 1984*b*). The eastern limit of this warm current north of Iceland vary from year to year, which explains why the largest fluctuations are found in the northeast. The temperature at Siglunes is, therefore, a good indicator of the ocean conditions north of Iceland.

It is clear that the ratio of grilse to salmon changes from time to time and long-term fluctuations can be seen in the ratio. The sea age of salmon seems to be determined in freshwater (Chadwick and Green 1985; Chadwick et al. 1986, 1987). The developmental rate of salmon is strongly genetically influenced (Thorpe 1986) but can be influenced by the environment (Thorpe 1977). The change in the grilse to salmon ratio could, therefore, change in two ways; the ratio changes in the stock in freshwater because of environmental changes there, or the survival at sea of either grilse and (or) salmon changes. It is highly likely that both explanations are valid when long-term changes are observed. In general, it seems that the salmon ratio increases in warmer periods and decreases in the colder periods (Figs. 3 and 5). These findings are in accordance with the results of Martin and Mitchell (1985) for the River Dee in Scotland. They associated the higher proportion of multi-sea-winter fish with subarctic ocean conditions; that is, in warmer years the salmon were able to migrate further north, but in colder years they were confined to more southerly and warmer location and matured earlier. Scarnecchia et al. (1989*c*, 1991) found significant positive correlation of the spring temperature and the grilse ratio in the smolt cohort entering the sea for some northwestern rivers and concluded that the growth rate of the smolt would increase at sea and that, therefore, the ratio would change. In those papers it is assumed that the decision of sexual maturation occurs in the marine environment. On the other hand it is possible that the age at maturity is determined in fresh water. In warmer periods the smolt would migrate to sea at younger age and return in higher proportion as salmon.

Table 2. Correlation coefficients of mean temperature at Siglunes and Latrabjarg, the salmon count in River Blanda and the salmon catch from 6 other rivers in Iceland for the smolt cohorts 1981–1990.

	Temperature at Latrabjarg	Temperature at Siglunes	Blanda	Vididalsa	Laxa i Adaldal	Sela	Hofa	Nordura	Thvera
Temperature at Latrabjarg									
Temperature at Siglunes	−0.37ns								
Blanda	−0.38ns	0.52ns							
Vididalsa	−0.18ns	0.66*	0.52ns						
Laxa i Adaldal	−0.45ns	0.65*	0.85**	0.66*					
Sela	−0.53ns	0.82*	0.73*	0.68*	0.79*				
Hofsa	−0.48ns	0.84*	0.87***	0.66*	0.82***	0.93***			
Nordura	−0.31ns	−0.91***	−0.36ns	−0.50ns	−0.52ns	−0.65*	−0.65*		
Thvera	−0.52ns	−0.49ns	−0.42ns	−0.20ns	−0.52ns	−0.46ns	−0.46ns	0.65*	

Note: Level of significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant.

Table 3. Correlation coefficients of the salmon ratio in the spawning run in River Blanda and in the catch from 6 other rivers in Iceland in the smolt cohorts 1981–1990.

	Blanda	Vididalsa	Laxa i Adaldal	Sela	Hofa	Nordura	Thvera
Blanda							
Vididalsa	0.79**						
Laxa i Adaldal	0.78**	0.78**					
Sela	0.16ns	0.26ns	0.01ns				
Hofsa	0.06ns	0.06ns	−0.01ns	0.85**			
Nordura	0.82**	0.87**	0.68*	−0.01ns	−0.29ns		
Thvera	0.67*	0.57ns	0.41ns	−0.24ns	−0.42ns	0.87**	

Note: Level of significance: *, $p < 0.05$; **, $p < 0.01$; ns, not significant.

The opposite would happen in colder periods, when older smolt and more sexually mature salmon would be leaving the rivers and returning in higher proportion as grilse. This could explain what seems to be contradictory findings.

These periodic changes observed in the salmon ratio make all catch forecasting using the grilse–salmon regression relationship difficult, and if it is used it should be done with caution using sufficient confidence limits.

If short-term changes are examined it is more likely that different survival rates are occurring at sea in the two components, grilse and salmon. Cold sea with low primary production and low abundance of zooplankton is considered to be unfavourable. For example, the smolt cohort entering the sea in 1983 in northern Iceland (Figs. 3 and 8) experienced very cold and unfavourable marine condition and the conditions (Anonymous 1992) were unfavourable all the time while the grilse were staying at sea (Fig. 6). This resulted in low return rates of that smolt class in general because of heavy mortality early after ocean migration (Figs. 2 and 7). Conditions improved in 1984 and were good in 1985 (Anonymous 1992) and resulted in high survival of salmon in their second year at sea (Figs. 2, 3, 7, and 8). The situation was similar for the 1979 smolt class (Fig. 3). The 1987 smolt class encountered favourable condition all the time when the grilse stayed at sea (Anonymous 1992) resulting in high return rates of grilse in 1988. In the fall of 1988 the conditions became unfavourable when polar current became dominant in the sea north of Iceland (Anonymous 1992) (Fig. 6), resulting in poor survival of the salmon component in the rivers of northern Iceland (Figs. 7 and 8). Large changes in the salmon ratio from 23 to 72% in the Blanda stock indicate that mortality of the salmon in the second year at sea can be very high. If it is assumed that the mortality in the 1983 smolt class during their second year at sea was 20% (number commonly used in fisheries science), the mortality was 88% for the 1987 smolt class during its second year at sea. To get the minimum number of deaths during the second year at sea for the 1987 smolt class it can be assumed that no mortality occurred during the second year at sea for the 1983 smolt class, which yields 68% mortality for the 1987 smolt class during the second year at sea. In all these calculations it is assumed that for each river, the smolt class have similar predetermined ratio of prospective grilse and salmon for short periods. This assumption is supported by the work of Chadwick et al. (1986, 1987) and by the fact that there is highly significant linear relation of grilse and salmon despite varying oceanic condition.

Fig. 7. Number of grilse (solid bars) and salmon (open bars) in the spawning run to Blanda and in the catch in the other rivers from the smolt cohorts 1981–1990.

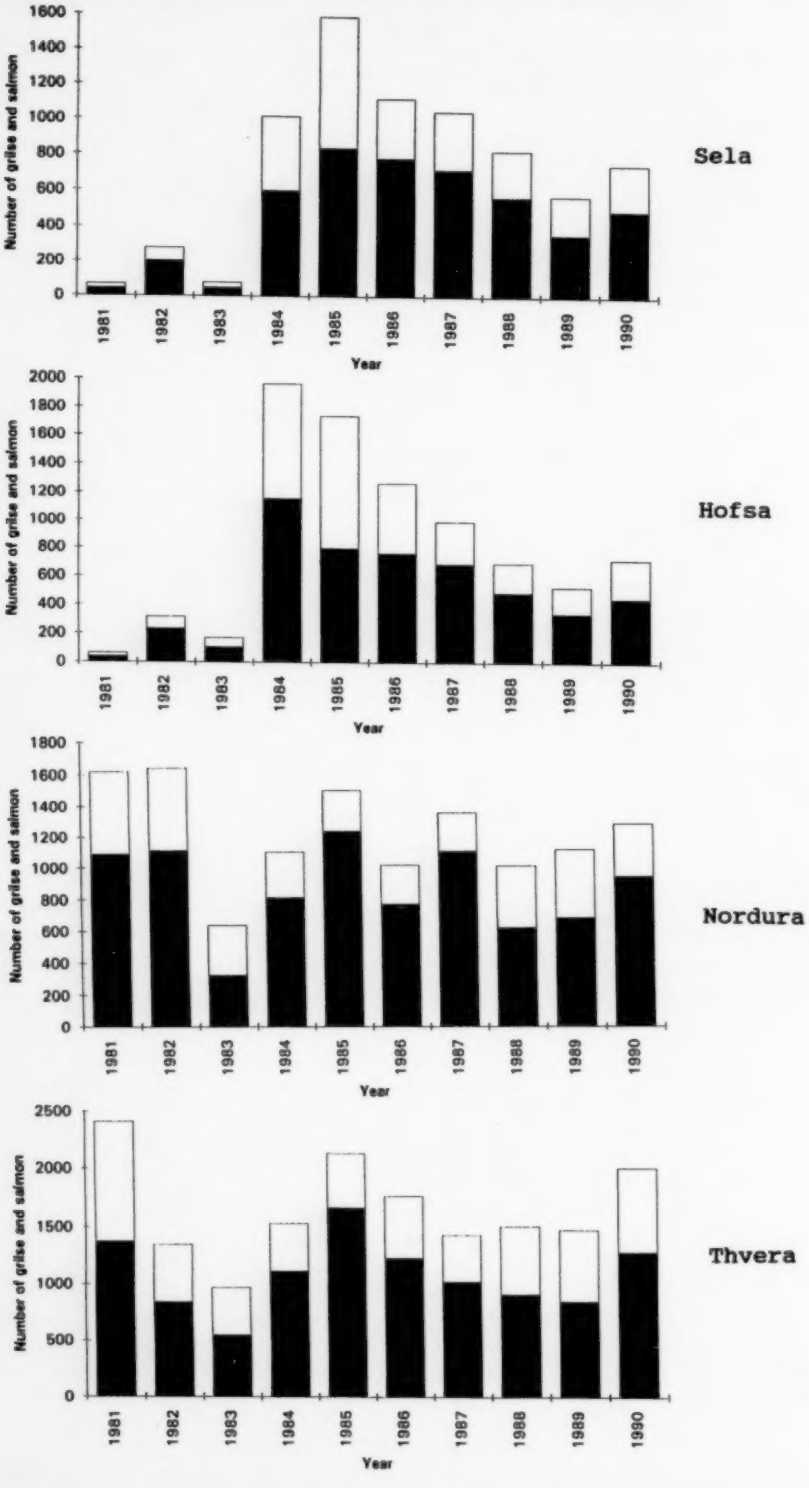
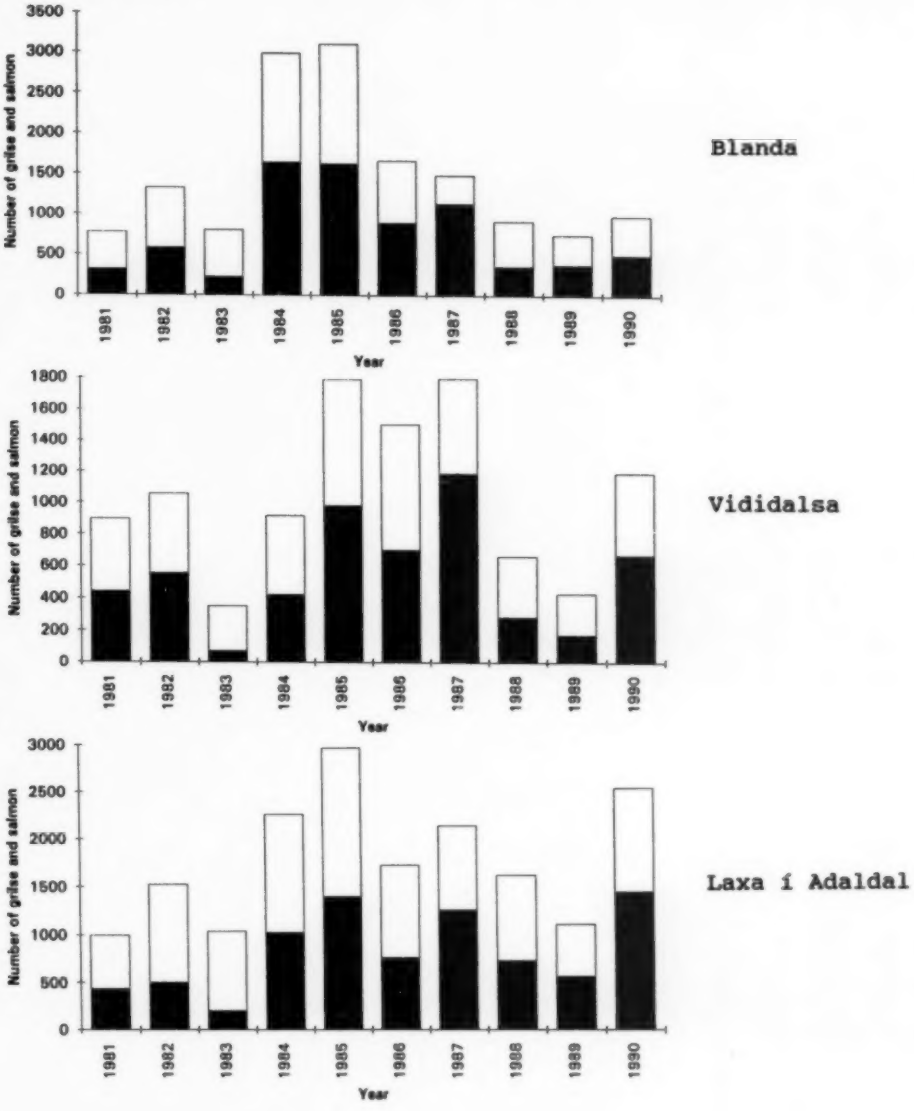


Fig. 7 (*concluded*).



The salmon ratio in all the rivers in northern Iceland change in a similar fashion (Fig. 8), indicating that these changes occur at sea or that some common climatic events influence the developmental rate of the salmon juveniles in all the rivers in the area. Jonasson et al. (1994) found that mortality rates for the second year at sea for the 1988–1990 smolt classes in an ocean ranching station in southwestern Iceland ranged from 54 to 65%. Tomasson et al. (1987) found similar mortality for the smolt classes 1979–1982 in the same ranching station. These findings were all conducted on smolt classes experiencing unfavourable marine conditions and agree with the high mortality rate in unfavourable years that the results in present study indicate.

Unfavourable oceanic conditions result in lower primary production and general reduction of food items for salmon and also for their predators. However, predators on salmon on their second year at sea must be few even though squid (Mills 1989) and seals (Rae and Shearer 1965) have been reported as predators. Food shortage could thus be the prime reason for the high mortality in some years.

In years with low temperature the abundance of grilse was lower in all the rivers examined, but the influence were more pronounced in the north and northeast. Salmon abundance also changed with temperature in the north and northeast, indicating that the Siglunes temperature gives

Fig. 8. The proportion of grilse (solid bars) and salmon (open bars) in the smolt cohorts 1981–1990 from the total run in River Blanda and the catch in other rivers.

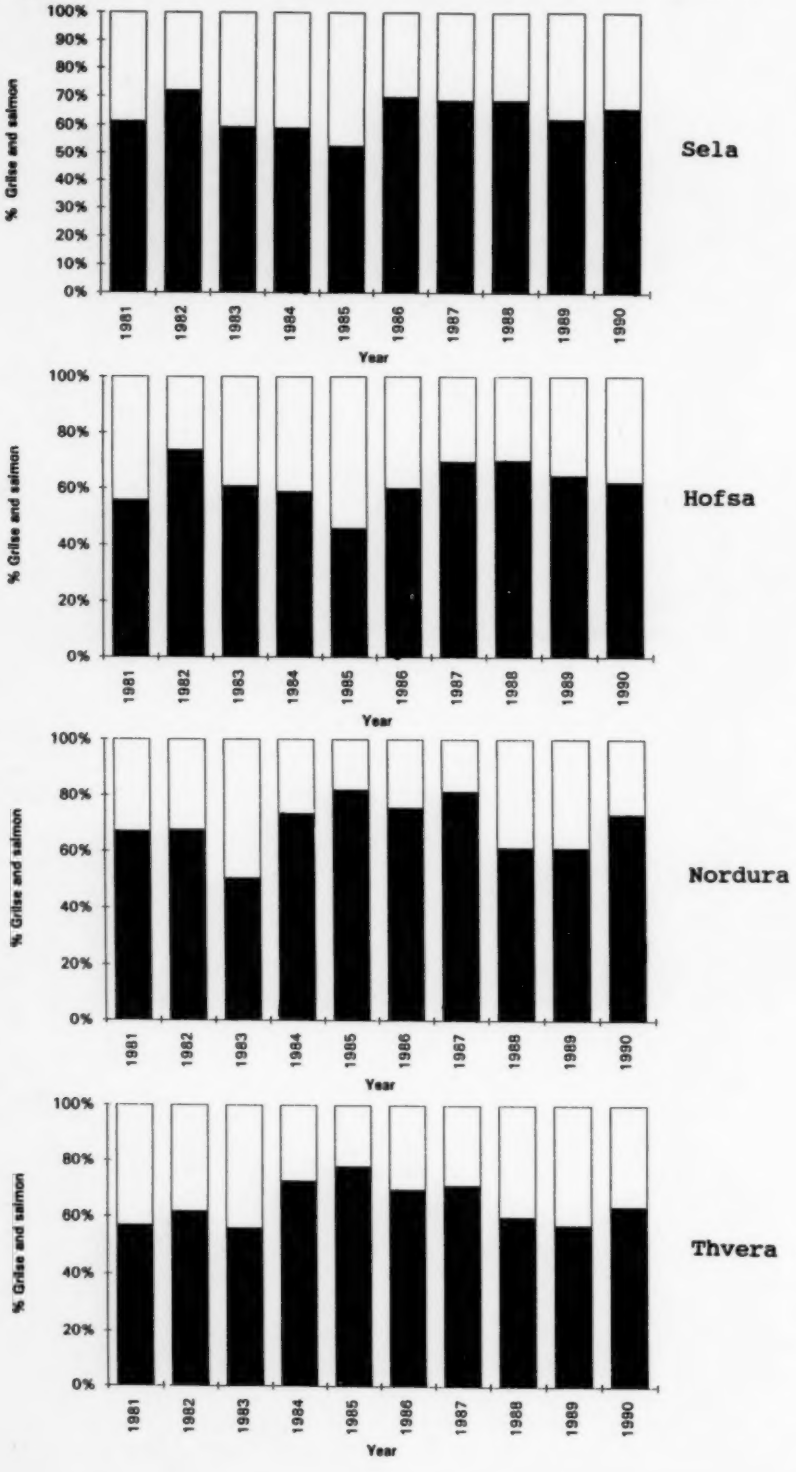
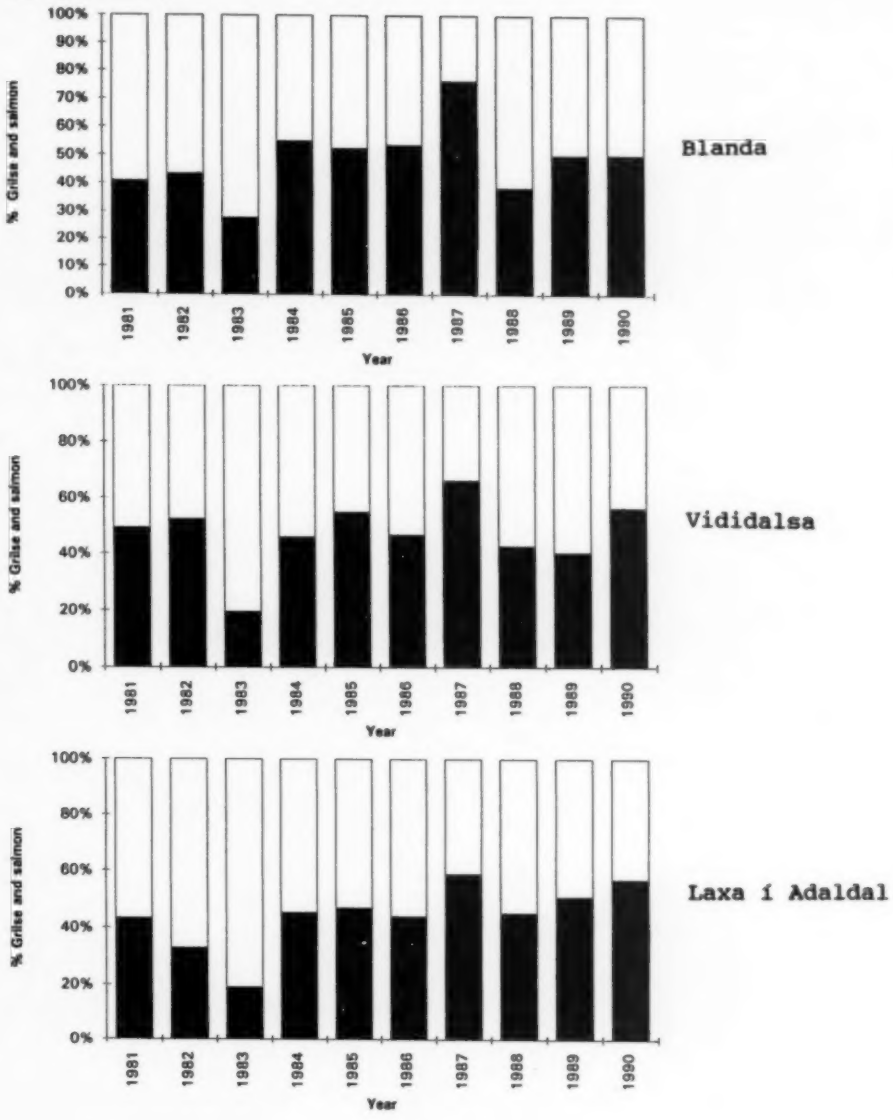


Fig. 8 (*concluded*).



some information on conditions where the salmon are staying in their second year at sea. The salmon in western Iceland must stay in another area with different conditions because the abundance there is not or even negatively correlated with the number of salmon in the north. Information on the long term conditions in the sea west of Iceland are badly needed because the Latrabjarg transect northwest of Iceland cannot explain the observed differences. Tagged salmon from western Iceland have been caught at western Greenland and tagged salmon from northern Iceland have been caught in the Faroese fishery. Furthermore, salmon from northwestern Iceland have been caught at eastern Greenland (Gudjonsson 1989). Our results support the idea that salmon in western Iceland are staying in the sea west of Iceland, salmon from northeastern Iceland stay in the sea east of Iceland, but salmon in northern Iceland could migrate to both of these areas. If this is true it could explain the differences in the salmon abundance and the salmon ratio observed in the three areas: western, northern, and northeastern Iceland. It is also possible that an ocean fishery can have some influence on the ratio, but any major effects of the Faroese and at Greenland fisheries have been ruled out (Scarnecchia et al. 1989*c*, 1991).

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References

Anonymous. 1992. Nytjastofnar sjavar og umhverfisthaettir 1991. Aflahorfur fiskveidiarid 1992/93. Marine Research Institute, Reykjavík, Iceland. Rep. 29. (In Icelandic).

Antonsson, Th., and S. Gudjonsson. 1993*a*. Rannsoknir a fiskistofnum vatnasvids Ellidaanna 1992. Institute of Freshwater Fisheries, Reykjavík, Iceland. Rep. 93014X. (In Icelandic).

Antonsson, Th., and S. Gudjonsson. 1993*b*. Vesturdalsa 1992. Gonguseidi, endurheimtur og thettleiki smaseida. Institute of Freshwater Fisheries, Reykjavík, Iceland. Rep. 93017X (In Icelandic).

Astthorsson, O.S., I. Hallgrimsson, and G.S Jonsson. 1983. Variations in zooplankton densities in Icelandic waters in spring during the years 1961–1982. J. Mar. Res. Inst. Reykjavik, 7: 73–113.

Box, D.E.P., and G.M. Jenkins. 1976. Time series analysis: forecasting and control. Holden-Day, San Francisco. 575 p.

Chadwick, E.M.P. 1988. Relationship between Atlantic salmon smolts and adults in Canadian rivers, p. 301–324. *In* D. Mills and D. Piggins [ed.] Atlantic salmon. Plans for the future. Timber Press, Portland, Oreg.

Chadwick, E.M.P., and J.M. Green. 1985. Atlantic salmon (*Salmo salar* L.) production in a largely lacustrine Newfoundland watershed. Verh. Int. Ver. Theor. Angew. Limnol. 22: 2509–2515.

Chadwick, E.M.P., R.G. Randall, and C. Leger. 1986. Ovarian development of Atlantic salmon (*Salmo salar*) smolts and age of first maturity, p. 15–23. *In* D.J. Meerburg [ed.] Salmonid age of first maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89.

Chadwick, E.M.P., R.R. Claytor, and C.E. Leger. 1987. Inverse correlation between ovarian development of Atlantic salmon (*Salmo salar*) smolts and sea age. Can. J. Fish. Aquat. Sci. 44: 1320–1325.

Gudbergsson, G., and F. Arnason. 1993. Laxveidin 1992. Institute of Freshwater Fisheries Reykjavík, Iceland. Rep. 93016. 18 p. (In Icelandic).

Gudjonsson, Th. 1978. The Atlantic salmon in Iceland. J. Agric. Res. Icel. 10: 11–39.

Gudjonsson, Th. 1989. Merktir laxar utan Islands. Institute of Freshwater Fisheries 89035. (In Icelandic).

Jonasson, J., V. Johannsson, and S. Oskarsson. 1994. Ocean mortality of ranched Atlantic salmon during the second year in the sea. Nord. J. Freshwater Res. 69: 79–83.

Kristjansson, J. 1982. Athugun a veidiskyrslum ur nokkrum laxveidiam NA- of A-lands 1969–1981. Aegir, 75: 121–126. (In Icelandic).

Malmberg, S.A. 1986. The ecological impact of the East Greenland current on the North Icelandic waters, p. 390–404. *In* S. Skerslet [ed.] The role of freshwater outflow in coastal marine ecosystems. NATO ASI Ser. G. Springer-Verlag, Berlin, Heidelberg.

Martin, J.H.A., and K.A. Mitchell. 1985. Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. Sci. 42: 1513–1521.

Mills, D. 1989. Ecology and management of Atlantic salmon. Chapman & Hall, London. 351 p.

Mundy, P.R., M. Alexandersdottir, and G. Eiriksdottir. 1978. Spawner–recruit relationship in Ellidaar. J. Agric. Res. Iceland. 10: 47–57.

Norusis, M.J. 1993. SPSS for windows. Base system users guide, release 6.0 edition. SPSS Inc. 828 p.

Rae, B.B., and W. Shearer. 1965. Seal damage to salmon fisheries. Mar. Res. 2. 39 p.

Reddin, D.G. 1988. Ocean life of Atlantic salmon in the Northwest Atlantic, p. 483–511. *In* D. Mills and D. Piggins [ed.] Atlantic salmon. Plans for the future. Timber Press, Portland, Oreg.

Scarnecchia, D. 1983. Age at sexual maturity in Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 40: 1456–1468.

Scarnecchia, D. 1984*a*. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon. Can. J. Fish. Aquat. Sci. 41: 917–945.

Scarnecchia, D. 1984*b*. Forecasting yields of two-sea-winter Atlantic salmon (*Salmo salar*) from Icelandic rivers. Can. J. Fish Aquat. Sci. 41: 1234–1240.

Scarnecchia, D. 1989. The history and development of Atlantic salmon management in Iceland. Fisheries (Bethesda, Md.), 14(2):14–21.

Scarnecchia, D., A. Isaksson, and S. White. 1989*a*. Ocean and riverine influences on variations in yield among Icelandic stocks of Atlantic salmon. Trans. Am. Fish. Soc. 118: 484–494.

Scarnecchia, D., A. Isaksson, and S. White. 1989*b*. Effects of oceanic variations and the West Greenland fishery on age at maturity of Icelandic west coast stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 46: 16–27.

Scarnecchia, D., A. Isaksson, and S. White. 1989*c*. New and revised catch forecasts for two-sea-winter Atlantic salmon (*Salmo salar*) in Icelandic rivers. J. Appl. Ichthyol. 5: 101–110.

Scarnecchia, D., A. Isaksson, and S. White. 1991. Effects of the Faroese long-line fishery, other oceanic fisheries and oceanic variations on age at maturity of Icelandic north-coast stocks of Atlantic salmon (*Salmo salar*). Fish. Res. (Bethesda, Md.), 10: 207–228.

Stefansson, U. 1961. Hafid. Almenna Bokafelagid, Reykjavik. 293 p. (In Icelandic).

Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing condition. J. Fish. Biol. 11: 1175–1184.

Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting, p. 7–14. *In* D.J. Meerburg [ed.] Salmonid age of first maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89.

Tomasson, T., A. Isaksson, and S. Oskarsson. 1987. Ocean mortality of ranched salmon during the second year in the sea. Smolts released 1979–1982. Report presented to the ICES ANACAT Working Group on Atlantic salmon, 9–20 Mar. 1987, Copenhagen.

Application of the bomb radiocarbon chronometer to the validation of redfish *Centroberyx affinis* age

John M. Kalish

Abstract: Validation of methods used to estimate fish age is a critical element of the fish stock assessment process. Despite the importance of validation, few procedures are available that provide unbiased estimates of true fish age and those methods that are available are seldom used. The majority of these methods are unlikely to provide an indication of the true age of individual fish, data that are best suited to the validation process. Accelerator mass spectrometry analyses of radiocarbon in selected regions of *Centroberyx affinis* otoliths were used to validate the age estimation method for this species. Radiocarbon data from the otoliths of *C. affinis* with presumed birth dates between 1955 and 1985 described the increase in ocean radiocarbon attributable to the atmospheric detonation of nuclear weapons in the 1950s and 1960s. The results confirm the longevity of *C. affinis* and demonstrate the effectiveness of the bomb radiocarbon chronometer for the validation of age-estimation methods.

Résumé : La validation des méthodes employés pour estimer l'âge des poissons constitue un élément critique du processus d'évaluation des stocks. Malgré l'importance de cette validation, rares sont les procédures qui fournissent des estimations non biaisées de l'âge réel des poissons, et les méthodes existantes sont rarement utilisées. La majorité de ces méthodes sont peu susceptibles de donner une indication de l'âge réel des poissons pris individuellement, information qui convient le mieux au processus de validation. Le recours à la spectrométrie de masse par accélérateur pour mesurer le radiocarbone dans des zones données des otolithes de *Centroberyx affinis* a permis de valider la méthode d'estimation de l'âge pour cette espèce. Les données sur le radiocarbone dans les otolithes de *C. affinis* présumément nés entre 1955 et 1985 illustrent l'accroissement du radiocarbone dans l'océan attribuable aux essais atmosphériques d'armes nucléaires dans les années 1950 et 1960. Les résultats confirment la longévité de *C. affinis* et démontrent l'efficacité du recours au radiocarbone produit par les essais nucléaires pour valider les méthodes d'estimation de l'âge.
[Traduit par la Rédaction]

Introduction

Several procedures are used for age estimation of teleosts; however, the counting of zones on otoliths appears to be used most frequently. Numerous validation studies for a range of fish species support the application of otolith zone counts for the routine estimation of fish age (see Summerfelt and Hall 1987; Smith 1992; Secor et al. 1995), where validation refers to the process of estimating the accuracy of the age estimation method (Kalish et al. 1995).

Validation is considered to be an essential component of age estimation studies; however, validation is not always attempted or it is not completed satisfactorily (Beamish and McFarlane 1987). The most frequently employed methods for validation include: (1) mark–recapture studies in conjunction with the injection of a substance (e.g., oxytetracycline hydrochloride or strontium chloride) capable of marking calcified tissues; (2) analysis of length–frequency modes; (3) monitoring of strong year-classes; (4) marginal increment analysis; and (5) radiometric age estimation. Beamish and McFarlane (1987) suggested "... that validation of ages of older fish requires either a mark–recapture study or the identification of known-age fish in the population."

Among the methods identified above, only mark–recapture studies and radiometric age estimation are suitable to the validation of age for longer lived fish with maximum ages in excess of about 20 years. Tagging studies, the most commonly employed method of validation, are impractical for many species because of low rates of recapture, softness of tissues, depth of occurrence, and post-harvest processing strategies. Furthermore, most tagging studies only provide an indication of the time elapsed between tagging and recapture and they do not provide a measure of true fish age.

Radiometric age estimation based on the activity ratios of various naturally occurring radionuclides (e.g., $^{210}Pb/^{226}Ra$) is gaining acceptance as an age validation technique (Bennett et al. 1982; Campana et al. 1990; Fenton et al.

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Table 1. Fish and otolith data from *Centroberyx affinis* collected in March 1993 off

Sample No.	Sex	Fish length (cm)	Fish weight (g)	Otolith weight (mg)	Sample weight (mg)	$\delta^{13}C$ (‰, PDB)	$\Delta^{14}C$(‰)
12	M	27	500	955	18.5	−1.29	−60.7 ± 6.7
9	M	29	571	1025	21.6	−1.85	−59.4 ± 6.7
4	M	26	471	970	21.5	−1.35	−56.1 ± 7.7
23	F	29	651	1096	23.3	−1.24	−44.7 ± 7.6
18	F	32	853	1080	17.4	−0.94	−44.7 ± 7.4
35	M	25	432	817	24.3	−1.37	−21.3 ± 8.6
10	M	29	598	879	18.2	−1.48	−10.5 ± 7.4
15	M	28	645	913	25.5	−1.55	55.9 ± 7.3
26	F	28	559	912	15.4	−1.3	72.1 ± 7.8
44	M	27	497	775	21.8	−2.43	83.2 ± 7.8
24	F	33	971	1015	18.5	−2.68	90.9 ± 7.7
11	F	28	586	691	23.5	−1.6	88.8 ± 11.1
1	F	25	442	637	19.6	−0.63	105.9 ± 11.9
8	F	27	457	563	22.1	−1.58	117 ± 11.3
30	F	27	454	584	23.4	−1.5	128.6 ± 10.7
2	Imm	9.3	—	92	21.5	−1.34	80.8 ± 8.3

Note: Fish ages were estimated by five readers, with readers 4 and 5 each providing two estimates of Values of $\Delta^{14}C$, mean age, and mean birthdate are reported with ±1 SD. Sample weights indicate the of otolith growth for an individual fish.

1991). Although radiometric age estimation is capable of overcoming many of the shortcomings of previously mentioned validation techniques, there are some problems associated with key assumptions (Fenton and Short 1992) and the relatively low precision of the method. In addition, radiometric age estimation requires sample sizes of about 1 g, making it necessary to pool samples from several otoliths for each analysis. This precludes the ability to detect age estimation errors resulting from incorrect interpretation of zones in individual otoliths; however, the technique is well suited as a general indication of fish age.

A new technique of age validation, based on the bomb radiocarbon chronometer (Kalish 1993, 1995) overcomes some problems associated with other age validation procedures and makes it possible to estimate the absolute age of individual fish. The method is based on the quantification of anthropogenic radiocarbon in selected regions of otoliths. Atmospheric testing of nuclear weapons in the 1950s and 1960s resulted in a drastic increase in radiocarbon levels in both the atmosphere and the ocean, and some of this radiocarbon was incorporated into living organisms. The increase in ocean radiocarbon during the 1960s was so rapid that the changing levels of radiocarbon during those years can be used as a de facto time scale. Otoliths have been shown to retain a chemical record that may be interpretable as a complex function of variations in a fish's physiology and environment over time (Kalish 1990, 1991*a*). Among the constituents of otoliths, radiocarbon has been shown to be a good proxy for radiocarbon levels in seawater dissolved inorganic carbon (Kalish 1993). Therefore, given a known temporal variation of radiocarbon in the environment, it should be possible to relate radiocarbon levels measured in otoliths to time. Using accelerator mass spectrometry, it is possible to measure with high precision (errors <1%), levels of radiocarbon in samples that contain less than 0.5 mg of carbon (e.g., Vogel et al. 1989). Aragonitic otoliths are 12% carbon making it feasible to analyse radiocarbon levels in otolith samples that weigh less than 5 mg. For many commercially important fish species, the amount of otolith calcium carbonate deposited in the first year of life exceeds 5 mg. This makes it possible to analyse radiocarbon levels in selected regions of a fish's otolith, including that portion that was deposited within 1 year or less of birth. By selecting otoliths from fish with presumed birth dates during the bomb-related increase in ocean radiocarbon and analysing segments of the otolith formed soon after birth, the fish's true age can be estimated. Ultimately, these data can be used to validate a method of age estimation. Furthermore, this validation procedure provides an estimate of the age of a fish that is independent of the counting of otolith zones.

This study presents results from an investigation into the application of the bomb radiocarbon chronometer to the validation of the age estimation method for redfish *Centroberyx affinis*. Redfish are an important commercial species in the trawl fishery off southeastern Australia; however, little information is available on their biology (Kailola et al. 1993). Juveniles are collected by trawling in shallow coastal waters and the adults are found on the continental shelf and slope down to depths of at least 450 m (May and Maxwell 1986). In Australian waters, redfish reach a maximum size of about 40 cm fork length and are believed to be slow growing. Previous estimates of age based on the number of zones visible in whole otoliths produced maximum ages of 16 years (Diplock 1984), whereas recent age estimates, based on zones in otolith

Ulladulla, New South Wales, Australia.

Age (birth date) determined by reader							Mean age (years)	Mean birth date (years, A.D.)
1	2	3	4/1	4/2	5/1	5/2		
37 (1956)	39 (1954)	35 (1958)	37 (1956)	37 (1956)	38 (1955)	38 (1955)	37.3 ± 1.3	1955.7 ± 1.3
34 (1959)	35 (1958)	37 (1956)	37 (1956)	37 (1956)	35 (1958)	43 (1950)	36.9 ± 3.0	1956.1 ± 3.0
34 (1959)	33 (1960)	32 (1961)	34 (1959)	38 (1955)	34 (1959)	39 (1954)	34.9 ± 2.6	1958.1 ± 2.6
33 (1960)	33 (1960)	34 (1959)	33 (1960)	34 (1959)	33 (1960)	36 (1957)	33.7 ± 1.1	1959.3 ± 1.1
32 (1961)	31 (1962)	29 (1964)	31 (1962)	31 (1962)	31 (1962)	32 (1961)	31.0 ± 1.0	1962.0 ± 1.0
30 (1963)	30 (1963)	30 (1963)	30 (1963)	32 (1961)	30 (1963)	31 (1962)	30.4 ± 0.8	1962.6 ± 0.8
29 (1964)	30 (1963)	29 (1964)	29 (1964)	31 (1962)	29 (1964)	31 (1962)	29.7 ± 1.0	1963.3 ± 1.0
27 (1966)	27 (1966)	26 (1967)	27 (1966)	27 (1966)	27 (1966)	25 (1968)	25.7 ± 2.1	1967.3 ± 2.1
27 (1966)	26 (1967)	26 (1967)	27 (1966)	27 (1966)	27 (1966)	27 (1966)	26.7 ± 0.5	1966.3 ± 0.5
25 (1968)	25 (1968)	25 (1968)	24 (1969)	27 (1966)	24 (1969)	30 (1963)	26.6 ± 0.8	1966.4 ± 0.8
26 (1967)	26 (1967)	26 (1967)	26 (1967)	28 (1965)	26 (1967)	27 (1966)	26.4 ± 0.8	1966.6 ± 0.8
23 (1970)	23 (1970)	21 (1972)	23 (1970)	23 (1970)	23 (1970)	23 (1970)	22.7 ± 0.8	1970.3 ± 0.8
17 (1976)	19 (1974)	18 (1975)	18 (1975)	19 (1974)	18 (1975)	18 (1975)	18.1 ± 0.7	1974.8 ± 0.7
12 (1981)	13 (1980)	13 (1980)	12 (1981)	12 (1981)	12 (1981)	13 (1980)	12.4 ± 0.5	1980.5 ± 0.5
7 (1986)	7 (1986)	7 (1986)	8 (1985)	8 (1985)	8 (1985)	8 (1985)	7.6 ± 0.5	1985.4 ± 0.5
2 (1991)	2 (1991)	2 (1991)	2 (1991)	2 (1991)	2 (1991)	2 (1991)	2 ± 0	1991.0 ± 0

age. All age and birthdate estimates presented in the table are determined from counts of presumed annual increments in otolith thin sections. weight of otolith material separated for individual analyses of stable carbon and radiocarbon and are representative of less than the first year

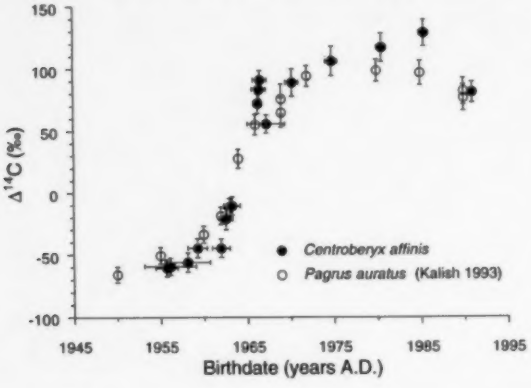
thin sections, indicate maximum ages in excess of 40 years (Smith and Robertson 1992). Because of their depth of occurrence and presumed age range, redfish are an ideal candidate for age validation based on the bomb radiocarbon chronometer.

Materials and methods

Sagittal otoliths from redfish were selected from archives at the Marine Science Laboratories, Queenscliff, Victoria, Australia. The samples selected were from redfish collected by commercial trawlers operating out of Uladulla (35°S, 151°E), New South Wales, Australia, in March 1993. One sagitta from each pair was embedded in polyester resin and four thin sections were taken in the transverse plane within the proximity of the otolith core. These sections were mounted on glass slides and the ages of fish were estimated by counting the number of presumed annual increments present. The otoliths were read by five independent readers to provide estimates of fish age. These age estimates were used as a guide to select otoliths for radiocarbon analysis. The greatest age resolution of the bomb radiocarbon chronometer is between about 1960 and 1974, the period when the rate of increase of radiocarbon in the ocean was greatest. For this reason, the majority of otoliths selected were from fish with presumed birth dates during those years. Otoliths from fish that were presumed to have been spawned prior to significant atmospheric testing of nuclear weapons were also selected to provide an indication of pre-bomb radiocarbon levels in the ocean off southeastern Australia and to provide an indication of the maximum fish age. Additional samples were also selected from redfish with presumed ages of less than 10 years to determine the peak in ocean radiocarbon in the region and to estimate the rate of loss of radiocarbon to other pools. Samples selected for analysis and age estimates based on thin sections are shown in Table 1.

Sample preparation procedures were similar to those described in Kalish (1993) for snapper, *Pagrus auratus*. Otolith aragonite deposited during a period presumed to be less than the first 8 months of life was isolated from one sagitta from each fish. This was accomplished by cutting and grinding the otolith with a hand-held high-speed drill to remove material deposited after what was presumed to be the first annual increment. Further grinding of the remaining portion of the otolith was used to "sculpt" the material into a structure with the shape and dimensions of the earliest formed portions of a redfish sagitta. Sagittae from very small redfish and zones visible on the otolith being sculpted were used as a guide. Counts of presumed daily increments in otolith thin sections suggested that the aragonite isolated for radiocarbon analyses may have been deposited in less than 8 months. Sample weights ranged from about 17 to 25 mg. Otolith carbonate was converted to CO_2 by reaction in vacuo with 100% phosphoric acid. An aliquot of the CO_2 was used to determine $\delta^{13}C$ for each sample and the remaining CO_2 was converted to graphite using excess H_2 and an iron catalyst (Lowe and Judd 1987). The graphatized samples were analysed for radiocarbon. Radiocarbon levels in each sample were determined by accelerator mass spectrometry (AMS) at the Institute of Geological and Nuclear Sciences, Lower Hutt, N.Z. (Wallace et al. 1987). Radiocarbon values are reported as $\Delta^{14}C$, which is the age- and fractionation-corrected deviation (in parts per thousand) from the activity of 19th century wood (Stuiver and Polach 1977). Age corrections are based

Fig. 1. $\Delta^{14}C$ of *Centroberyx affinis* otolith cores plotted against presumed birth date. $\Delta^{14}C$ data from *Pagrus auratus* otolith cores are plotted against the true birth date and the data are from Kalish (1993). Birth dates were estimated from otolith sections read by multiple readers. For both *C. affinis* and *P. auratus*, $\Delta^{14}C$ values are based on otolith material deposited over a time period less than the first year of life. Errors are ±1 SD.



on the mean estimate of age determined from reading of otolith sections. Radiocarbon determinations were made via the National Bureau of Standards oxalic acid standard in conjunction with the ANU sucrose standard. Reported errors are 1 SD for both radiocarbon data and age estimates based on the reading of otolith sections. Radiocarbon errors include both counting errors and laboratory random errors.

Results

The radiocarbon data obtained from redfish otoliths were plotted against the presumed birth date estimated from the otolith sections from the same fish (Fig. 1). These data were plotted with a time series of bomb radiocarbon data for temperate latitudes in the South Pacific determined from snapper otoliths (Kalish 1993) (Fig. 1). The radiocarbon data from snapper are used as a calibration between surface ocean radiocarbon levels measured at temperate latitudes in the southern hemisphere and time, as the snapper data are representative of the true variation in radiocarbon (Kalish 1993). On this basis, variations between radiocarbon levels for years/birth dates estimated from sections of redfish otoliths and radiocarbon levels determined from snapper otoliths are representative of possible errors in the estimation of birth date for individual redfish.

The change in radiocarbon level over time, as estimated from the redfish otoliths, describes a curve that is representative of the pre- and post-bomb flux of radiocarbon in the ocean and is consistent with data from snapper. Radiocarbon levels increased in the early 1960s because of the flux of bomb radiocarbon from the atmosphere to the ocean and these levels peaked after about 1975. In later years, the bomb-derived radiocarbon became redistributed to other carbon pools including organisms, sediments, dissolved organic carbon, and particulate organic carbon.

The majority of the redfish data fall within the curves defined by the upper and lower 95% confidence limits determined for individual predicted values from the snapper data. Redfish and snapper data from the period spanning the rapid increase of radiocarbon (1955–1980) were modelled separately with a cubic polynomial (Table 2). The cubic polynomial was selected a priori because it was most likely to represent the two inflections in radiocarbon levels due to anthropogenic inputs from atomic testing and the subsequent decrease in radiocarbon resulting from loss to other pools. All but three of the redfish data points fell within the 95% confidence limits determined from the snapper data and those three points were on, or just beyond, the curves defined by the confidence limits. The snapper confidence limits are fully enclosed by the confidence limits defined by the redfish data.

Discussion

Radiocarbon analyses of redfish otoliths indicate that increments visible in otolith thin sections form annually and that counting these increments is a valid method for estimating redfish age. The oldest fish in the sample were at least 33 years old based on pre-bomb radiocarbon levels measured in several otoliths and estimates of age based on counts of annual increments suggest that the oldest fish may have been over 37 years of age (Table 1). Using the bomb radiocarbon chronometer with redfish samples that are currently available, it is not possible to provide an unequivocal estimate of the maximum redfish age; it is possible only to determine that an individual fish was spawned prior to the flux of bomb radiocarbon into the temperate South Pacific Ocean around 1960. If later collections of redfish otoliths are made, for example in the year 2000, then the maximum age that could be estimated would be 40 years.

Three possible explanations for deviations between the snapper and the redfish data include: (1) errors in redfish age estimates determined from otolith thin sections; (2) differences in the uptake rates of carbon and, concomitantly, radiocarbon from the environment for the two species; and (3) differences in oceanographic and atmospheric circulation resulting in a different flux of radiocarbon in the snapper and redfish habitats. There may be some errors in the estimates of redfish age, but if errors do exist, they cannot be detected on the basis of the radiocarbon data presented in this study. There were three instances, however, where the section age birth date for redfish did not fall within the 95% confidence limits defined by polynomial regression of the snapper data between 1955 and 1980, (sample Nos. 18, 24, and 44). In addition, the redfish datum from 1985 (sample No. 30) appeared to deviate from the radiocarbon calibration curve; a possible explanation for this is discussed later.

One assumption that was made in the interpretation of the radiocarbon data obtained from fish otoliths was that there were no significant differences in the uptake rates of carbon containing ions between fish species. The

Table 2. Curvilinear regression results for radiocarbon versus birth date (year) data from snapper (*Pagrus auratus*) and redfish (*Centroberyx affinis*) between the years 1955 and 1980.

	n	r^2	Intercept	x	x^2	x^3	SE(x)	SE(x^2)	SE(x^3)
Pagrus auratus	10	0.97	2.82×10^8	-4.30×10^5	218.9	−0.037	1.22×10^5	62.1	0.010
Centroberyx affinis	14	0.91	3.04×10^8	-4.63×10^5	235.9	−0.040	2.33×10^5	118.4	0.020

potential sources of carbon to the $CaCO_3$ of the otolith include dissolved inorganic carbon from the seawater and organic carbon derived from food. Data are limited, however, there is evidence that a large percentage (>60%) of otolith carbon is derived directly from dissolved inorganic carbon in seawater (Kalish 1991*b*, 1991*c*). Regardless of the sources of otolith carbon, studies indicate that uptake rates for ions can vary among species (see Hoar and Randall 1984). The radiocarbon data, however, are unlikely to be adequate to resolve this variation.

There are distinct differences in ocean circulation between the habitats of the snapper and redfish used in this study and these differences are likely to result in detectable differences in the temporal variation in ocean radiocarbon. The snapper were from the east coast of the North Island of New Zealand and the redfish were collected off southeastern Australia, a separation of over 2000 km. Redfish live in a region of Southeastern Australia that is influenced by the East Australian Current, a major current that has its origin in tropical oceans and would be a rich source of bomb-derived radiocarbon. The snapper were collected in a region of New Zealand that is not characterized by strong currents, but it does derive some water from the region of the Tasman Front via the East Auckland Current (Heath 1985). These differences suggest that greater quantities of bomb radiocarbon may reach southeast Australia via ocean circulation.

Other studies on the flux of radiocarbon to the South Pacific Ocean indicated that a peak in surface ocean radiocarbon in the region occurred around 1974 (Landman et al. 1988; Toggweiler et al. 1991; Kalish 1993). These studies also showed a gradual decline, albeit at different rates, in ocean radiocarbon after 1974 as the radiocarbon became incorporated into other inorganic and organic carbon pools. The redfish radiocarbon data suggest that radiocarbon levels off the coast of New South Wales were still increasing up to 1985. Furthermore, the maximum $\Delta^{14}C$ value of 128.6 ± 10.7‰ (mean ± SD) from 1985 is significantly higher than the maximum value of 98.4 ± 8.8‰ measured for snapper from a similar latitude off New Zealand (Kalish 1993), but lower than peak $\Delta^{14}C$ values obtained from corals from Fiji (138‰) (Toggweiler et al. 1991) and Heron Island (145‰) (Landman et al. 1988). This result may be an indication of the relative transport of dissolved inorganic carbon from the Coral Sea to the coast of New South Wales via the East Australian Current. Other features of the radiocarbon time series based on the redfish otoliths might be explained on the basis of regional oceanography; however, given the fact that the majority of differences between the redfish and snapper data are not significant, these distinctions would not be well supported.

Application of the bomb radiocarbon chronometer to the estimation of fish age requires the existence of a calibration, such as the snapper data, so that temporal variations in radiocarbon for a particular region can be approximated. For many regions these data are lacking and the snapper data presented in Kalish (1993) represented the first pre- and post-bomb time series of radiocarbon at temperate latitudes. A similar time series for northern temperate latitudes was produced by Weidman and Jones (1993) on the basis of radiocarbon data obtained from shells of the bivalve *Arctica islandica*. Several radiocarbon time series obtained from tropical and subtropical hermatypic corals are available (e.g., Druffel and Linick 1978; Nozaki et al. 1978; Toggweiler et al. 1991). The available radiocarbon data, however, are not always adequate to provide an accurate estimate of radiocarbon in a particular region and, in some instances, the best data that are available are the single measurements of pre- and post-bomb radiocarbon made directly on seawater as part of programs such as the GEOSECS expeditions (e.g., Broecker et al. 1985). Despite the lack of calibration data in some regions, the bomb radiocarbon chronometer can still be extremely effective because of our basic understanding of the flux of radiocarbon in the marine enviroment. For example, the presence of very low levels of radiocarbon (i.e., less than −40‰) would indicate that the fish was born prior to 1960. Alternatively, a rapid increase in radiocarbon over time would provide a validation for a series of otoliths presumed to have birth dates between about 1960 and 1970, even in the absence of any calibration data. Of course, calibration curves can be developed for other regions using radiocarbon data obtained from otoliths where an independent validation of age is available; this was the strategy employed in developing the calibration based on snapper otolith radiocarbon (Kalish 1993).

The major limitations to the application of the bomb radiocarbon chronometer for age estimation include the requirement for otoliths from fish with birth dates between about 1960 and 1975 and complications in determining the environmental variation in radiocarbon experienced during early life for some deepwater or highly migratory species. Given the apparent range of ages for many commercially important species the requirement for samples from fish with birth dates between 1960 and 1975 is not always a problem. Furthermore, many fisheries laboratories maintain extensive otolith archives and this can make it possible to use the method for species with relatively short life spans. Although the method cannot determine accurately the age of fish spawned prior to 1960, the absence of bomb radiocarbon in a sample provides an indication that a fish is relatively long lived. In addition, increased

precision of radiocarbon estimates may make it possible to utilise the decrease in bomb radiocarbon, after about 1980, as a chronometer; however, this chronometer would be unlikely to provide the temporal resolution achievable during the 1960s and early 1970s.

It may be difficult or impossible to apply the bomb radiocarbon chronometer to some deep-sea or highly migratory fish species. The flux of bomb-derived radiocarbon to the deep sea may be very slow or, in some cases, undetectable. Some deepwater fish do have larval and juvenile stages that are present in surface waters and these species should be amenable to age estimation on the basis of bomb radiocarbon levels (Kalish 1995). Highly migratory species may be problematic because of difficulties in determining the region where the early growth stages of the fish took place.

The bomb radiocarbon chronometer is suitable for determining the absolute age of a range of fish species. Despite its utility, however, cost may prevent the application of the method in some situations. Typical costs for accelerator mass spectrometry analysis of radiocarbon in a single otolith sample are about CAN$650. This cost includes conversion of the sample to CO_2 and then graphite. Other procedures, including otolith sculpting, can be accomplished easily in most laboratories. The number of samples to be analysed is dependent on the degree of validation that is desired; achieving a very precise estimate of the accuracy of an age estimation method would, undoubtedly, be more costly. On the other hand, confirming the temporal meaning of the zones being counted is a critical part of the validation procedure that could be achieved with a single, carefully selected, radiocarbon analysis. Given the costs and time involved in completing a tagging study, the bomb radiocarbon chronometer represents a viable and cost-effective means of validation.

This study indicates the suitability of reading otolith sections to estimate the age of redfish and demonstrates the efficacy of age validation using the bomb radiocarbon chronometer. The procedure is rapid and relatively low cost, and provides data suitable for a complete validation of age estimation procedures. The radiocarbon data presented here can also be applied to investigations of carbon flux and ocean circulation.

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References

Beamish, R.J., and G.A. McFarlane. 1987. Current trends in age determination methodology. p. 15–42. *In* R.C. Summerfelt, and G.E. Hall [ed]. Age and growth of fish. Iowa State University Press, Ames, Iowa.

Bennett, J.T., G.W. Boehlert, and K.K. Turekian. 1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from Pb-210/Ra-226 measurements in otoliths. Mar. Biol. (Berlin), 71: 209–215.

Broecker, W.S., T.-H. Peng, G. Ostlund, and M. Stuiver. 1985. The distribution of bomb radiocarbon in the ocean. J. Geophys. Res. 90: 6953–6970.

Campana, S.E., K.C.T. Zwanenburg, and J.N. Smith. 1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47: 163–165.

Diplock, J.H. 1984. A synopsis of available data on redfish *Centroberyx affinis* from NSW waters. *In* Working Papers, DPFRG Workshop on Trawl Fish Resources, 27–29 Mar. 1984, Sydney, Australia. Unpublished report. Available from the Fisheries Research Institute, Cronulla, NSW, Australia.

Druffel, E.M., and T.W. Linick. 1978. Radiocarbon in annual coral rings of Florida. Geophys. Res. Lett. 5: 913–916.

Fenton, G.E., and S.A. Short. 1992. Fish age validation by radiometric analysis of otoliths. Aust. J. Mar. Freshwater Res. 43: 913–922.

Fenton, G.E., S.A. Short, and D.A. Ritz. 1991. Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae) using ^{210}Pb:^{226}Ra disequilibria. Mar. Biol. (Berlin), 109: 197–202.

Heath, R.A. 1985. A review of the physical oceanography of the seas around New Zealand—1982. N.Z. J. Mar. Freshwater Res. 19: 79–124.

Hoar, W.S., and D.J. Randall [Ed]. 1984. Fish physiology. Vol. 10. Part B. Ion and water transfer. Academic Press, Orlando, Fla.

Kailola, P.J., M.J. Williams, P.C. Stewart, R.E. Reichelt, A. McNee, and C. Grieve. 1993. Australian fisheries resources. Bureau of Resource Sciences and the Fisheries Research and Development Corporation, Canberra, Australia. 422 p.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. U.S. 88: 657–666.

Kalish, J.M. 1991*a*. Determinants of fish otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74: 137–159.

Kalish, J.M. 1991*b*. Oxygen and carbon stable isotopes in the otoliths of wild and laboratory-reared Australian salmon (*Arripis trutta*). Mar. Biol. (Berlin), 110: 37–47.

Kalish, J.M. 1991*c*. ^{13}C and ^{18}O isotopic disequilibria in fish otoliths: metabolic and kinetic effects. Mar. Ecol. Prog. Ser. 75: 191–203.

Kalish, J.M. 1993. Pre- and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. 114: 549–554.

Kalish, J.M. 1995. Radiocarbon and fish biology, p. 637–653. *In* D.H. Secor, J.M. Dean, and S.E. Campana [ed.] Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Kalish, J.M., R.J. Beamish, E.B. Brothers, J.M. Casselman, R.I.C.C. Francis, H. Mosegaard, J. Panfili, E.D. Prince, R.E. Thresher, C.A. Wilson, and P.J. Wright. 1995. Standard terms for otolith research, p. 723–729. *In* D.H. Secor, J.M. Dean, and S.E. Campana [ed.] Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Landman, N.H., E.R.M. Druffel, J.K. Cochran, D.J. Donahue, and A.J.T. Jull. 1988. Bomb-produced radiocarbon in the shell of the chambered nautilus: rate of growth and age at maturity. Earth Planet. Sci. Lett. 89: 28–34.

Lowe, D.C., and W.J. Judd. 1987. Graphite target preparation for radiocarbon dating by accelerator mass spectrometry. Nucl. Instrum. Methods, B28: 113–116.

May, J.L., and J.G.H. Maxwell. 1986. A field guide to trawl fish from the temperate waters of Australia. CSIRO Division of Fisheries Research, Hobart, Australia. 492 p.

Nozaki, Y., D.M. Rye, K.K. Turekian, and R.E. Dodge. 1978. A 200-year record of carbon-13 and carbon-14 variations in Bermuda coral, Geophys. Res. Lett. 5: 825–828.

Secor, D.H., J.M. Dean, and S.E. Campana [Ed]. 1995. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C. 735 p.

Smith, D.C. [Ed]. 1992. Age determination and growth in fish and other aquatic animals. CSIRO, Melbourne, Australia. 458 p.

Smith, D.C., and S.G. Robertson. 1992. Age determination for redfish, *Centroberyx affinis*, from samples submitted to the Central Ageing Facility: 1991/1992. Marine Science Laboratories, Queenscliff, Victoria, Australia. Internal Rep. 203.

Stuiver, M., and H. Polach. 1977. Reporting of ^{14}C data. Radiocarbon, 19: 355–363.

Summerfelt, R.C., and G.E. Hall [Ed]. 1987. Age and growth of fish. Iowa State University Press, Ames, Iowa. 544 p.

Toggweiler, J.R., K. Dixon, and W.S. Broecker. 1991. The Peru upwelling and the ventilation of the South Pacific thermocline. J. Geophys. Res. 96: 20 467–20 497.

Vogel, J.S., D.E. Nelson, and J.R. Southon. 1989. Accuracy and precision in dating microgram carbon samples. Radiocarbon, 31: 145–149.

Wallace, G., R.J. Sparks, D.C. Lowe, and K.P. Pohl. 1987. The New Zealand accelerator mass spectrometry facility. Nucl. Instrum. Methods, B29: 124–128.

Weidman, C.R., and G.A. Jones. 1993. A shell-derived time history of bomb ^{14}C on Georges Bank and its Labrador Sea implications. J. Geophys. Res. 98: 14 577–14 588.

Spatial and temporal variation in littoral-zone benthic invertebrates from three south-central Ontario lakes

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Abstract: Surveys of benthic invertebrates have revealed patterns attributed to the impacts of acid deposition. Unfortunately, these patterns may be confounded by temporal variation that will affect follow-up studies of the recovery of these communities. Here, we assess spatial and temporal variation in time-limited, kick-and-sweep collections of littoral-zone benthos. Spatial variation comprised five sites representing the predominant nearshore substrates in each of three lakes. Temporal variation spanned a different scale in each lake with five sites sampled: (*i*) twice on the same day, (*ii*) once a week for 3 weeks, and (*iii*) four times through the ice-free season. Variation was quantified using a model II analysis of variance. Spatial differences predominated in same-day samples (60.4% of the variation on average) and those collected over a 3-week period (46.1%). In contrast, samples collected over the ice-free season revealed that spatial and temporal factors accounted for 9.4 and 25.6% of the variation. We conclude that our collections of littoral macrobenthos are highly repeatable if sampling is restricted to short periods (e.g., 3 weeks). Surveys spanning longer periods may incorporate considerable temporal variation from seasonal changes in abundance.

Résumé : Des relevés des invertébrés benthiques ont révélé des profils attribuables aux impacts des dépôts acides. Malheureusement, ces profils peuvent être brouillés par des variations temporelles qui affectent les études de suivi concernant le rétablissement de ces communautés. Nous évaluons ici la variation spatiale et temporelle des prélèvements de benthos de la zone littorale effectués en temps limité par perturbation du fond et balayage. La variation spatiale couvrait cinq sites représentant les substrats qui prédominaient près de la rive dans chacun des trois lacs. La variation temporelle couvrait une échelle différente pour chaque lac, dont les cinq sites ont été échantillonnés : (*i*) deux fois le même jour; (*ii*) une fois par semaine pendant 3 semaines; (*iii*) quatre fois pendant la saison libre de glace. La variation a été quantifiée à l'aide d'une analyse de variance de modèle II. Les différences spatiales prédominaient dans les échantillons du même jour (60,4% de la variation en moyenne) et dans les échantillons recueillis sur une période de 3 semaines (46,1%). Par contre, dans le cas des échantillons prélevés pendant toute la saison libre de glace, les facteurs spatiaux et temporels expliquaient 9,4 et 25,6% de la variation. Nous concluons que nos échantillons de macrobenthos littoral sont hautement reproductibles si le prélèvement est restreint à de courtes périodes (p.ex., 3 semaines). Les relevés couvrant des périodes plus longues peuvent présenter des variations temporelles considérables liées aux changements saisonniers de l'abondance.

[Traduit par la Rédaction]

Introduction

Communities of benthic macroinvertebrates are commonly used as long-term biomonitors of the health of aquatic ecosystems (Wilhm and Dorris 1968; Barton 1989; France 1990). In areas subject to periodic discharges of anthropogenic contaminants, intolerant taxa disappear and tolerant species dominate the community (Harman 1974; Nalepa and Thomas 1976; Okland and Okland 1979; Lauritsen et al. 1985; Mackie 1989). As a result, the composition of the benthic community depends on the available habitat and various predators, the frequency and types of anthropogenic and natural disturbances, and the recolonization and competitive abilities of the component species (Roback 1974; McAuliffe 1984; Okland and Okland 1986). If habitat differences are minimized, periodic faunal surveys provide snapshots of the benthic community that should correlate with the recent history of water and sediment quality (e.g., Nalepa and Thomas 1976; Dermott et al. 1986; Poulton et al. 1988).

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Surveys of benthic macroinvertebrates of small lakes in south-central Ontario have revealed differences in benthic communities that have been attributed to changes in lake pH associated with acid deposition (Roff and Kwiatkowski 1977; Collins et al. 1981; Harvey and McArdle 1986; Stephenson and Mackie 1986; Stephenson et al. 1994). Unfortunately, large-scale surveys often mix the effects of seasonal changes in abundances with differences in abundances that are attributed to spatial patterns in, for example, water chemistry. Depending on the survey design, seasonal variation may be misidentified as spatial variation (Malley and Reynolds 1979). As a result, geographic patterns become either blurred or enhanced, possibly leading to erroneous inferences (Bivand 1980). Follow-up surveys designed to reveal long-term changes in communities attributable to reductions in anthropogenic contaminants may also be confounded by seasonal variation (e.g., Rabeni et al. 1985). In most benthic studies, the relative magnitudes of spatial and temporal variation are rarely quantified (cf. Peterson 1975; Davis and van Blaricom 1978; Wright 1992).

Standard bioassessment protocols that utilize benthic macroinvertebrates (e.g., Plafkin et al. 1989; Klemm et al. 1990; Gibbons et al. 1993) now include routine quality assurance – quality control (QA/QC) checks to ensure data integrity. Quality assurance procedures involve documented standard operating procedures, comprehensive data recording, management, and verification protocols, as well as regular performance evaluation (Plafkin et al. 1989; Klemm et al. 1990). By contrast, quality control procedures focus on data quality through the establishment of data quality objectives that specify limits for data accuracy, precision, and completeness to guarantee that the resultant data are truly representative and comparable (Klemm et al. 1990; Gibbons et al. 1993).

Extrapolating QA/QC results to field data is often difficult. Although QA/QC procedures are not new in field (e.g., Furse et al. 1981; Pollard 1981; Mackey et al. 1984) or laboratory (e.g., Ettinger 1984) studies, the findings are usually summarized in separate documents with limited applicability (e.g., Clifford and Casey 1992). Occasionally, estimates of data accuracy and precision are used to evaluate the power of sampling designs (i.e., the ability to detect a change) (e.g., Downing and Downing 1992; Morin and Cattaneo 1992) or the optimal sample size (e.g., Cuff and Coleman 1979; Downing and Cyr 1985). Recently, Pollard and Peck (1991) advocated the use of model II analysis of variance (ANOVA) to quantitatively evaluate QA/QC data on a scale that is commensurate with field data. This use of variance components directly links QA/QC and field data given an appropriate experimental design (e.g., Bailey and Byrnes 1990). Moreover, the use of ANOVA permits the separation of complex patterns, such as seasonal variation that may be nested within an overall annual trend, from random variation associated with sampling and measurement error.

Herein, we use model II ANOVA in a QA/QC context to assess the magnitude of spatial and temporal variation in our estimates of the relative abundance of macroinvertebrates in the littoral zones of three small lakes. We sampled the littoral benthos with a fixed-time, kick-and-sweep protocol. Fixed-time sampling has been criticized because the area covered will vary according to habitat and water conditions, as well as the individual who collects the sample (Elliott 1977, pp. 126–128; Furse et al. 1981; Pollard 1981; Lenat 1988). Consequently, many benthic ecologists presume that abundance data expressed per unit time are inferior to abundances measured per unit area. The goals of this study are (*i*) to quantitatively evaluate spatial and temporal variation in collections of benthic macroinvertebrates to assess the repeatability and relative precision of our sampling protocol, (*ii*) to identify a sampling time frame where temporal variability is less than within-lake spatial variation, and (*iii*) to identify those major taxonomic groups that are sampled with high repeatability and high precision. Our analysis revealed that our sampling protocol produced highly repeatable short-term results. As the sampling period was lengthened, the importance of spatial relative to temporal variation declined to the point where differences among samples collected every 6 weeks were dominated by seasonal changes in the abundances of most taxonomic groups.

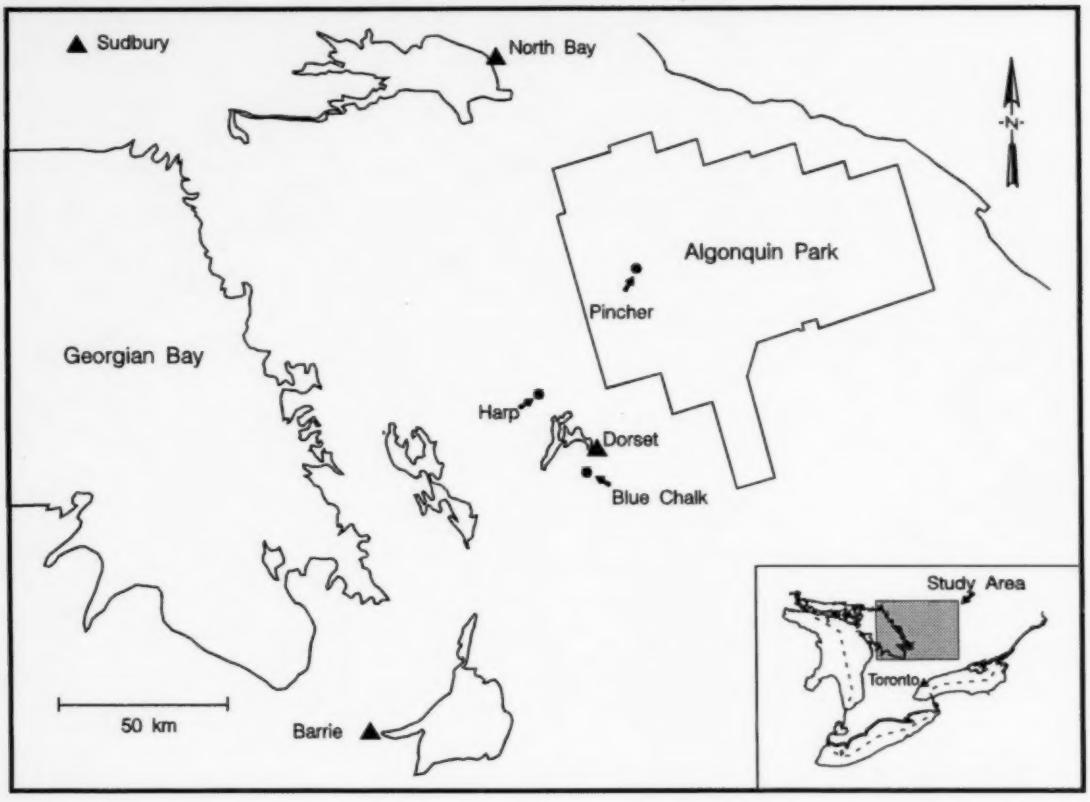
Methods

In 1988, we initiated a biomonitoring programme to assess long-term trends in the composition of benthic invertebrate communities in acid-sensitive, soft-water Precambrian Shield lakes (Reid et al. 1994*a*). This work is part of the federal–provincial Long-Range Transport of Airborne Pollutants (LRTAP) programme that is designed to assess anticipated changes in the health of inland aquatic ecosystems associated with reductions in sulphur emissions (Shaw et al. 1992). A standard survey protocol is currently used by members of the LRTAP programme to permit comparisons among data sets collected from six areas in eastern Canada.

We undertook this study to evaluate the repeatability and relative precision of our sampling protocol. Herein, we define repeatability as the temporal variance component that is the proportion of the total variation in abundance attributable to different sampling times (e.g., Lewis 1978, and see below). Over protracted time periods this temporal variance component will incorporate seasonal changes in abundance (i.e., temporal autocorrelation). By contrast, we define relative precision as the coefficient of variation (CV) expressed as the standard deviation in abundance divided by the mean (e.g., Grossman et al. 1990). Separate CVs were calculated for the spatial and temporal effects (see below). Recently France (1992) challenged the utility of our protocol because the relative precision associated with timed kick-and-sweep samples is generally unknown (cf. Furse et al. 1981; Mackey et al. 1984). If this precision is poor, our biomonitoring programme may be unable to detect temporal changes when contrasted with approaches using absolute abundances of indicator species (Lenat 1988; Lauritsen et al. 1985; Rabeni et al. 1985; Stephenson and Mackie 1986).

Pincher, Harp, and Blue Chalk lakes are small headwater lakes located on the Precambrian Shield in south-central Ontario, Canada (Fig. 1). Dillon et al. (1987) found that lakes in this region are susceptible to acidification from inputs of atmospheric pollutants because of the low-carbonate geological nature of the watersheds. The average

Fig. 1. Map of south-central Ontario indicating the location of the three study lakes.



pH of these lakes over the ice-free season ranged from 5.8 for Pincher Lake to 6.6 for Blue Chalk Lake (Table 1). The invertebrate fauna of these three lakes is assumed to be representative of acid-sensitive, softwater lakes (e.g., Collins et al. 1981; Dermott et al. 1986; Stephenson et al. 1994). We anticipate that this faunal assemblage will change in response to water quality improvements arising from reductions in SO_2 emissions.

In an initial survey, the field crew circumnavigated each lake and recorded the relative frequencies of various substrate types between the shore and a depth of approximately 1 m. Five sites were then randomly selected to represent the predominant substrates: typically rocks and boulders, silt and (or) sand with macrophytes, and silt covered with detritus and woody debris (Table 1). The frequency of each type of site (e.g., one rocky, one sand, two silt with detritus) was proportional to the prevalence of each type of nearshore substrate in a given lake (for further details see Reid et al. 1994*a*).

Five sites in Pincher Lake were sampled on May 5, 1988. Because our protocol destructively samples an area, paired samples were collected from adjacent areas at each site to estimate variability when temporal effects were presumed to be negligible. To examine short-term temporal variation, the littoral macrobenthos was sampled once each week for 3 weeks at five sites in Harp Lake (i.e., April 25, May 2, and May 10, 1988). Samples were also collected from five sites in Blue Chalk Lake every 6–10 weeks for a total of four dates (i.e., May 9, June 20, September 1, and November 2, 1988) to assess the relative importance of temporal variation over the ice-free season. Spatial variation attributed to differences among the five sites was assumed to be similar in each lake, although differences in the predominant substrate types were observed (Table 1).

Sampling methods

Because of site-specific differences in habitat complexity, we collected benthic invertebrates with a kick-and-sweep method standardized to a constant period of time rather than a standard unit of area (e.g., Okland and Okland 1979; Furse et al. 1981; Stephenson et al. 1994). This method usually collects a large percentage of all species in proportion to their abundance with relatively few samples (Elliott 1977; Mackey et al. 1984). As a result, fixed-time sampling provides information on relative abundance and species occurrence whereas areal sampling estimates absolute abundance.

Benthic invertebrates were collected for 10 min along several transects (0–1 m depth) located 5 m apart within each site by using a standard D-frame, 250-μm mesh net

Table 1. Physical and chemical characteristics of the three south-central Ontario lakes.

Lake	Latitude	Longitude	Elevation (m)	Area (ha)	Mean depth (m)	Maximum depth (m)	pH	Alkalinity (μequiv./L)	Substrates at each site[a]		
									Type 1	Type 2	Type 3
Pincher	45°34′	78°51′	511	42.1	6.1	15.5	5.8	3	2,3	1	4,5
Harp	45°23′	79°07′	329	71.4	13.3	37.5	6.3	10	2	1,3,4	5
Blue Chalk	45°12′	78°56′	336	52.4	8.5	23.0	6.6	80	2	1,5	3,4

[a]Substrate types: 1, rock and boulder; 2, silt and (or) sand with macrophytes; 3, silt covered with detritus and woody debris.

(Reid et al. 1994*a*). On each transect the collector waded out to a depth of 1 m. The substrate was gently kicked to disturb and dislodge the surface sediment and associated detritus. The disturbed material was swept up with the net and transferred to a plastic bucket as the collector waded slowly towards the shore. At each site a number of transects were sampled until 10 min had elapsed. The resultant sample from each site was labelled, refrigerated, and transported to our laboratory for further processing within 24 h.

At the laboratory, the samples were sieved through 6250- and 1000-μm mesh to separate the coarse detritus and large invertebrates from the finer material. The >1000-μm fraction and any invertebrates retained by the 6250-μm mesh were preserved in 70% ethanol. The >1000-μm fraction was stained with a mixture of water-soluble Eosin B and Biebrich Scarlet to assist in removing the remaining macroinvertebrates from the debris. The samples were stained for 2 days, washed, and then sorted for 4–6 h to remove all of the remaining animals. The resultant samples of benthic invertebrates were identified to the lowest practical taxonomic level. In most instances, the taxonomic resolution was to the genus or species level (e.g., see Reid et al. 1994*a*, 1994*b*).

Data analysis

The initial taxon-by-site-by-time matrices for each lake consisted of a large number of taxa that were found at only one site or during one sampling period. Unfortunately ANOVA and many multivariate methods are unduly influenced by the large numbers of zeros arising from rare taxa in these types of data matrices (Oksanen 1983; Minchin 1987; ter Braak and Prentice 1988). A number of methods have been proposed to eliminate rare taxa that contribute very little to the marginal totals of the data matrix. For example, Orloci (1975) and Jancey (1979) suggested selecting taxa on the basis of their redundancy or their ability to distinguish a priori groups of sites. Alternatively, rules of thumb such as taxa found in fewer than five samples or taxa represented by fewer than 10 individuals can be invoked to discard rare taxa (e.g., Gauch 1982; Oksanen 1983). Unfortunately, these approaches disproportionately remove taxa identified to the species level, whereas taxa identified to coarser taxonomic levels generally consist of larger numbers of individuals and hence are not omitted. As a result, we chose to combine species into coarser taxonomic groups. Our final data sets consisted of total counts of approximately 20–30 major taxonomic groups (e.g., see Table 2) tabulated by site and by sampling date. In this way, we agglomerated rather than subjectively discarded data. Hilsenhoff (1988) and Warwick (1988) found that relatively coarse taxonomic resolution, even at the family level, will reveal dominant patterns in the data from faunal surveys.

For each lake, spatial and temporal variation were assessed by comparing the total number of individuals (i.e., total counts) in each taxonomic group using a two-way, model II ANOVA (SAS Institute Inc. 1988). Among-site spatial variation and among-time temporal variation were summarized as variance components representing variation attributable to these two main effects (e.g., Lewis 1978; Matthews 1990). These two variance components were standardized to proportions that sum to equal the total variance explained by the two-way ANOVA. Because replicate samples were not collected within sites or times, the interaction between sites and times was the error term in the ANOVA. A large error term (or small percentage of the variance explained) reflects a large degree of sampling imprecision (described as ephemeral spatial variation by Lewis (1978)). In contrast, taxa with large spatial variance components display site-to-site differences in abundance that may be attributable to strong habitat affinities. Taxa with large temporal variance components display considerable differences in abundance between sampling periods (perhaps as a result of life-history events), and hence have low sampling repeatability. Consequently, variance components provide standardized estimates of spatial variation (e.g., within-lake differences in habitat affinity), temporal variation (i.e., sampling repeatability), and sampling error (i.e., the percentage of the variance not explained). Further descriptions of model II ANOVA are presented in standard biometric texts (e.g., Sokal and Rohlf 1981, pp. 191–207; Krebs 1989, pp. 453–458).

Both raw and logarithmically transformed (i.e., log $(N + 1)$) data were analyzed with model II ANOVA. If results from the log-transformed data differed from those of the raw data, we assumed that the raw data failed the parametric assumptions of the ANOVA (e.g., normality and homogeneity of variance). However, raw and log-transformed data generally provided similar results. Consequently, we report variance components for the analysis accounting for the largest proportion of the total variance of a particular taxon.

Differences among taxa were illustrated by plotting spatial variation (i.e., variation attributed to site differences) versus the percentage of the total variance explained by the two-way ANOVA model (see Fig. 2). Those taxa with large amounts of their total variation in abundance

Table 2. Relative abundances of the major taxonomic groups over differing sampling periods.

Taxon code[a]	Taxon name	Relative abundances per sampling period[b]								
		Pincher Lake		Harp Lake			Blue Chalk Lake			
		1	2	1	2	3	1	2	3	4
	Turbellaria	A	A	A	R	R	A	A	P	A
1	Nematoda	P	P	P	R	R	R	R	R	R
2	Oligochaeta	C	C	C	C	C	C	C	C	C
3	Hirudinea	R	R	P	R	R	P	R	A	P
4	Amphipoda	F	F	F	F	F	F	F	F	F
	Decapoda	A	A	A	A	A	A	P	P	P
5	Hydracarina	A	A	R	C	R	P	P	P	A
	Collembola	P	A	A	A	A	P	A	A	A
6	Ephemeroptera	F	F	F	F	F	F	C	C	F
7	Odonata	C	C	C	C	F	C	R	C	C
	Plecoptera	P	A	P	R	A	A	A	A	P
8	Hemiptera	R	R	R	R	A	P	P	A	A
	Megaloptera	P	P	P	R	A	P	A	P	A
9	Trichoptera	C	C	C	C	C	R	R	C	C
10	Lepidoptera	P	A	P	R	R	P	A	P	P
11	Coleoptera	R	R	R	R	C	C	C	C	C
12	Diptera									
	Total	F	F	F	F	F	F	F	F	F
13	Ceratopogonidae	C	C	F	F	F	F	C	C	C
14	Chironomidae	F	F	F	F	F	F	F	F	F
	Podonominae	A	A	P	A	A	A	A	A	P
15	Tanypodinae	F	F	F	F	F	F	F	F	F
16	Prodiamesinae	A	A	P	R	R	P	A	A	P
17	Orthocladiinae	F	F	F	F	F	C	F	C	F
18	Chironominae	F	F	F	F	F	F	F	F	F
19	Chironomini	F	F	F	F	F	C	F	C	F
20	Tanytarsini	F	F	C	F	F	C	F	F	F
	Tabanidae	P	A	A	R	A	P	A	A	A
	Tipulidae	A	A	R	R	P	P	A	A	R
21	Gastropoda	A	A	C	C	C	P	R	R	P
22	Pelecypoda	C	P	C	F	C	R	R	C	R

[a]Code used to designate taxa in figures; those taxa without codes were not used in subsequent analyses.
[b]A, absent; P, present (<5 individuals collected per lake); R, rare (5–25 individuals collected per lake); C, common (25–100 individuals collected per lake); F, frequent >100 individuals collected per lake.

"explained" by the ANOVA (e.g., lying to the right of the 50% point on the *x* axis) are sampled with little error. Taxa lying near the 1:1 line have relatively high sampling repeatability (i.e., a small temporal variance component). In contrast, taxa lying near the 1:2 line exhibit equal proportions of temporal and spatial variation. Those taxa that lie near the *x* axis have poor repeatabilities because temporal variation predominates.

As a complement to our measure of repeatability, we assessed sampling precision by calculating CVs across sites and across times. In this context, CVs were calculated for each site on the basis of variation among samples collected at different times. These five CVs were averaged to produce a mean temporal CV. Similarly, CVs were calculated for each sampling period and then were averaged to generate a mean spatial CV. In this way, average CVs were compared to determine whether greater precision was associated with spatial or temporal factors. Those taxa with relatively large temporal CVs (say arbitrarily >30%) and large error variances from the two-way ANOVA were sampled inefficiently. In contrast, taxa with small temporal CVs (say <30%) and small proportions of their total variance explained by the two-way ANOVA may be sampled efficiently, but the small spatial and temporal variance components indicate low repeatability. Taxa with small temporal CVs and large spatial variance components are sampled with high precision and high repeatability.

Warwick and Clarke (1991) proposed that multivariate summaries were more sensitive than univariate and bivariate statistics for detecting broad community-based patterns of change, and hence that multivariate analyses were often superior to traditional univariate and bivariate approaches.

As a result, we summarized multivariate trends in the benthic community with correspondence analysis (CA) (Rohlf 1988; Hill 1974; Gauch et al. 1977; Minchin 1987). This technique reduced our count data organized by sites and times, and by taxon, into ordination axes that summarize the predominant trends of variation. The resultant site-by-time scores on the first three axes were assumed to represent the major multivariate trends in the proportional abundances of the benthic community (i.e., CA essentially works with the percentages of each taxonomic group in each site at each time; Doledec and Chessel 1991). Because CA can be distorted by columns or rows with a large number of zeros (Oksanen 1983; Ezcurra 1987; ter Braak and Prentice 1988), we omitted those major taxonomic groups represented by less than 10 individuals and present in fewer than five samples from the ordination analysis. The taxa contributing most to the CA axes were inferred from correlations between their original abundances and the scores on the new axes. We tabulated both Pearson product-moment and Spearman rank correlations between the abundances of the major taxonomic groups and the ordination (site by time) scores to assist in this interpretation. However, we relied on the nonparametric rank statistics because these correlations are more robust to outliers (given the small sample sizes). Subsequently, scores on the first three CA axes were analyzed in a two-way ANOVA to partition variation in the benthic community according to spatial and temporal factors as above. In addition, analogues of the spatial and temporal CVs were calculated to contrast precision on the basis of the multivariate community summary. Here we used the standard deviation (SD) of the CA scores for a particular site or time divided by the SD for all the points on the axis. CVs were not used because the CA axis scores were already centered to an overall mean of zero. These SDs were then averaged to provide estimates of temporal or spatial variation within each ordination axis.

Results

Samples collected on the same day

Of the 23 major taxonomic groups collected from Pincher Lake, six groups were classified as very rare, being represented by less than five individuals in a given sampling period (Table 2). Nine groups, including the Amphipoda, Ephemeroptera, and most of the Diptera, were classified as frequent with more than 100 individuals/collection. Taxa with the largest temporal CVs were the Hirudinea, Coleoptera, Tanypodinae, Pelecypoda, Trichoptera, and Ephemeroptera, respectively (Table 3). In contrast, temporal CVs for 8 of the other 11 taxa were less than 30%, suggesting that these 8 groups were sampled with precision. Moreover, all but two of the spatial CVs were larger than the corresponding temporal CVs. Because the temporal replicates represent small-scale spatial variation (between paired or "split" samples) relative to among-site spatial variation, this result indicated that site-related differences in the counts of most taxa exceeded variation among paired samples collected on the same day.

The total variance explained by the two-way ANOVA ranged from 0% for Hirudinea (3) and Ephemeroptera (6) to almost 90% for Oligochaeta (2), Coleoptera (11),

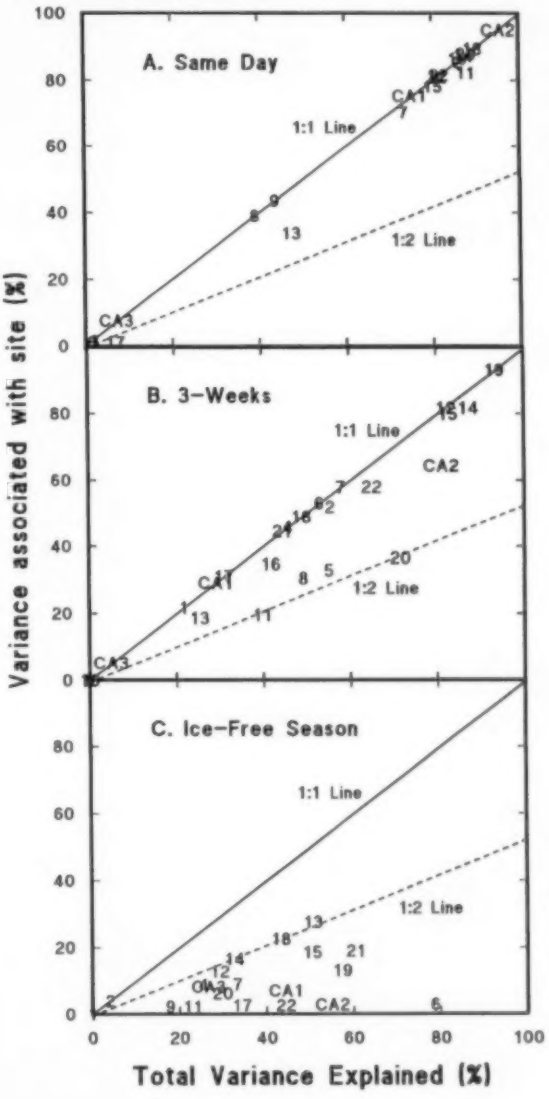


Fig. 2. Plot of the spatial variance component with respect to the total variance explained from the two-way ANOVA for the major taxonomic groups. Numbers represent the taxonomic groups identified in Table 2. The 1:1 line indicates where spatial effects predominate; the 1:2 line indicates where spatial and temporal factors account for equal amounts of the total variance incorporated by the two-way ANOVA. Temporal variation is most important for those taxa lying near the *x* axis.

Chironomidae (14), Chironominae (18), Chironomini (19) and Tanytarsini (20) (the numbers refer to these taxa in Fig. 2). Temporal variance components attributed to replicate samples collected on the same day ranged from 0 to 13.6%, with an average of 1.9%. In contrast, spatial variation associated with differences among sites ranged from 0

Table 3. Average temporal and spatial coefficients of variation (CVs in %) for the major taxonomic groups.

Taxon	Average temporal CVs			Average spatial CVs		
	Daily (2)	Weekly (3)	Monthly (4)	Daily (2)	Weekly (3)	Monthly (4)
Nematoda	—	75.94	103.68	—	112.10	101.48
Oligochaeta	31.98	53.25	75.51	82.45	81.14	78.97
Hirudinea	87.01	—	—	85.17	—	—
Amphipoda	31.64	45.19	46.03	71.27	61.61	38.25
Hydracarina	—	87.37	—	—	95.12	—
Ephemeroptera	40.72	66.57	116.96	51.09	95.63	62.02
Odonata	27.49	41.34	87.34	48.09	74.32	63.47
Hemiptera	27.27	106.60	—	71.06	102.16	—
Trichoptera	43.05	73.27	90.49	58.89	64.03	69.58
Coleoptera	47.08	76.79	63.64	108.28	71.07	70.91
Diptera						
Total	19.39	31.70	49.84	44.07	73.56	48.82
Ceratopogonidae	23.95	49.27	77.23	30.72	65.46	73.65
Chironomidae	21.59	31.17	54.30	50.39	83.75	54.12
Tanypodinae	45.23	32.14	64.44	73.84	68.95	56.19
Prodiamesinae	—	141.74	—	—	156.81	—
Orthocladiinae	32.62	57.37	67.24	31.16	96.34	58.14
Chironominae	21.57	58.76	58.82	58.39	118.23	68.62
Chironomini	24.13	49.13	83.32	57.97	139.48	60.42
Tanytarsini	18.01	88.16	67.88	67.51	67.60	81.08
Gastropoda	—	59.03	168.60	—	84.54	176.97
Pelecypoda	43.69	52.46	87.98	111.08	69.66	70.86
CA 1	34.08	58.56	81.33	99.32	99.71	70.51
CA 2	16.75	46.79	83.51	98.32	88.10	57.75
CA 3	53.14	82.38	78.94	99.95	94.91	74.77

Note: Dashes in otherwise empty cells indicate that a taxon was absent from that lake. CV analogues (as relative SDs in %) for the three CA axes are listed below the taxa.

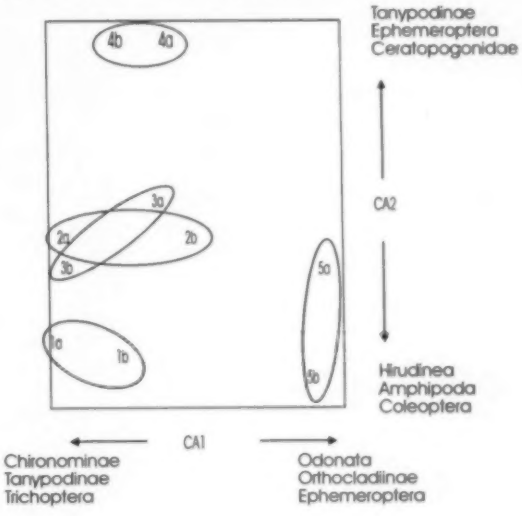
to 89.4%, with an average of 60.4%. These results emphasize that among-site spatial effects accounted for the largest differences in the counts of most taxa. This variation is probably associated with habitat-related differences among the five sites. In the graphical summary (Fig. 2*a*), taxa exhibit temporal variation in proportion to their distance below the 1:1 line. For example, Coleoptera (11) and Ceratopogonidae (13) exhibited the largest relative amounts of temporal variation. Consequently, counts of these taxa have lower repeatability than the other taxa using our kick-and-sweep protocol. Taxa with a relatively large proportion of their total variance associated with spatial differences exhibited high repeatability. For example, counts of Oligochaeta (2), Amphipoda (4), Odonata (7), Chironomidae (14), Tanypodinae (15), Chironominae (18), and Pelecypoda (22) exhibited large site effects and thus high repeatabilities. Hemiptera (8), Trichoptera (9), and Ceratopogonidae (13) exhibited intermediate amounts of spatio-temporal variation, whereas virtually no spatial or temporal variation was evident in the Hirudinea (3), Ephemeroptera (6), and Orthocladiinae (17). Of these latter taxa, the Hirudinea, Ephemeroptera, and Trichoptera had large temporal CVs, suggesting considerable unexplained variation attributable to sampling error (see Table 3).

To investigate whether the major trends in the benthic community had high repeatability, we examined the first three axes from the CA ordination of the counts of the 13 major taxonomic groups collected from Pincher Lake. The site-by-time-by-taxon matrix exhibited significant structure (chi-square = 1453.9 with 108 df, $P < 0.001$), and the resultant CA summarized 85.5% of the overall variation in the benthic community in the first three axes (i.e., 51, 25, and 10%, respectively). The two-way ANOVA indicated significant spatio-temporal separation on the second axis (CA2; $F = 18.1$, $P < 0.008$) with differences approaching significance on the first (CA1; $F = 5.08$, $P < 0.07$), but not the third axis (CA3; $F = 0.86$, $P < 0.567$). These differences are illustrated by the separation of the two samples from site 4 from the samples from other sites along CA2, whereas CA1 distinguishes site 5 from the other sites (Fig. 3). Odonata, Orthocladiinae, and Ephemeroptera, respectively, had the largest positive correlations with CA1 (Table 4). These taxa were most abundant at site 5. In contrast, Chironominae, Tanypodinae, and Trichoptera exhibited the largest negative correlations with CA1. Amphipoda, Hirudinea, and Coleoptera were negatively correlated with CA2, whereas Tanypodinae, Ephemeroptera, and Ceratopogonidae were positively

correlated with that axis. Thus, the benthic community at site 4 was characterized by lower abundances of Amphipoda, Hirudinea, and Coleoptera, and higher abundances of Tanypodinae, Ephemeroptera, and Ceratopogonidae relative to the other sites.

The SDs for each of the three CA axes also emphasized that temporal variation was less than spatial variation (Table 3). This pattern is evident in the plot (Fig. 3) with samples collected from the same site lying in close proximity. The variance components revealed that the benthic community represented by the first two CA axes had high repeatability, with spatial variation accounting for 72 and 91% of the variation in those axes, respectively, and temporal variation of 0 and 1% (Fig. 2*a*). By contrast, the temporal SDs were 34 and 17% on CA1 and CA2 whereas the spatial SDs were 99 and 98% of the overall SD for each axis. According to the variance-components analysis, CA3 failed to resolve spatial or temporal variation among the samples collected on the same day. However, the SDs indicated that relative temporal variation on CA3 was approximately half (53%) of the relative spatial variation (100%; see Table 3).

Fig. 3. Plot of the site scores for the first two axes from the correspondence analysis of the data collected on the same day. Ellipses surround the daily (2) samples from each of the five sites highlighting the predominant site (spatial) effects revealed by the ANOVA.



Samples collected over a 3-week period

The two-way ANOVA for the three collections from Harp Lake also revealed that spatial or habitat-related factors accounted for the greatest proportion of the variance (Fig. 2*b*). As before, the spatial variance component (i.e., site effects) was plotted against the total variance explained by the two-way ANOVA. The 1:1 and the 1:2 lines highlight where spatial factors predominate (i.e., those taxa lying near the 1:1 line) and where spatial and temporal factors account for approximately equal proportions of the total variance (i.e., those taxa near the 1:2 line). Any taxa where temporal variation predominated would lie near the *x* axis.

At this 3-week sampling scale, the total variance explained by the two-way ANOVA ranged from 0% for Trichoptera (9) to more than 80% for the total Diptera (12), Chironomidae (14), Tanypodinae (15), and Chironomini (19) (Fig. 2*b*). Temporal variation ranged from 0 to 35% with an average of 6.5%. Spatial and temporal variance components for Coleoptera (11) and Tanytarsini (20) were almost equal (i.e., these two taxa lie near the 1:2 line in Fig. 2*b*). By contrast, spatial effects predominated in all of the other taxa (average of 46.1%), although the total variance explained was generally lower than that for the same-day samples (i.e., 52.5 versus 62.3%). Those taxa with more than 50% of the total variance explained by the two-way ANOVA and where spatial variation exceeded temporal variation were sampled with high repeatability. These taxa included the Oligochaeta (2), Hydracarina (5), Ephemeroptera (6), Odonata (7), total Diptera (12), Chironomidae (14), Tanypodinae (15), Chironomini (19), Tanytarsini (20), and Pelecypoda (22) (see Fig. 2*b*).

Spatio-temporal factors accounted for relatively small amounts of the variation in the counts (i.e., <50%; see Fig. 2*b*) of the Nematoda (1), Amphipoda (4), Hemiptera (8), Trichoptera (9), Coleoptera (11), Ceratopogonidae (13), Prodiamesinae (16), Orthocladiinae (17), Chironominae (18), and Gastropoda (21). Only the total Diptera, total Chironomidae, and Tanypodinae had temporal CVs approaching 30% (Table 3). All other taxa were collected with relatively poor precision over the 3-week period (i.e., CVs > 40%). Spatial CVs exceeded temporal CVs for all but four of the major taxonomic groups (i.e., Hemiptera, Trichoptera, Coleoptera, and Tanytarsini), suggesting that variation associated with differences among the sites was generally greater than temporal variation over the 3-week sampling period.

The matrix of counts based on triplicate samples from each of the five sites in Harp Lake exhibited significant structure (chi-square = 2533.4 with 224 df, $P < 0.001$). The resultant CA summarized 69.9% of the variation in the first three axes. CA1 and CA2 incorporated similar proportions of the total variation (30 and 25%, respectively). As before, the two-way ANOVA explained a significant amount of the variation on CA2 ($F = 9.24$, $P < 0.003$), but not CA1 or CA3 ($F = 1.50$, $P = 0.289$ and $F = 0.20$, $P = 0.966$, respectively). Site effects accounted for 64% of the variation on CA2 and 29.1% on CA1, whereas temporal effects were only evident on CA2 (16.6%, see Fig. 2*b*). In contrast, both spatial and temporal variance components on CA3 were zero.

Samples were weakly clustered by site on the first two axes of the ordination (Fig. 4). In particular, sites 2 and 5 were distinct on CA2. Two groups of samples were evident along CA1, but samples from sites 2 and 3 were found in both groups. The rank correlations between the abundances and the site scores (Table 5) indicated that sites 2 and 5 had relatively few Tanypodinae, Odonata, and Orthocladiinae and more Ceratopogonidae relative to the other three sites. These differences corresponded with

Table 4. Loadings (correlations) of the major taxonomic groups on the first three CA axes on the basis of samples collected on the same day.

	Pearson's correlation			Spearman's correlation		
Taxon	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Oligochaeta	−0.341	−0.379	0.400	−0.220	−0.067	0.457[a]
Hirudinea	0.245	−0.553[a]	0.456	0.180	−0.626[a]	0.303
Amphipoda	0.612[a]	−0.550[a]	−0.225[a]	0.382	−0.637[a]	−0.418[a]
Ephemeroptera	0.340[a]	0.442[a]	0.469[a]	0.479[a]	0.503[a]	0.200
Odonata	0.869[a]	0.084	−0.213	0.835[a]	−0.097	−0.323[a]
Hemiptera	−0.082	0.503[a]	0.184	0.199	0.220	−0.081
Trichoptera	−0.630[a]	0.213	0.520[a]	−0.596[a]	0.190	0.559[a]
Coleoptera	−0.475	−0.387	0.625[a]	−0.333	−0.444[a]	0.710[a]
Ceratopogonidae	−0.135	0.068	−0.576[a]	0.091	0.286[a]	−0.371[a]
Tanypodinae	−0.705[a]	0.513[a]	−0.265[a]	−0.649[a]	0.527[a]	−0.200
Orthocladiinae	−0.257	0.130	0.139	0.579[a]	0.177	0.146
Chironominae	−0.818[a]	−0.278	0.122	−0.855[a]	0.006	0.224
Pelecypoda	−0.338	−0.456[a]	0.122	−0.274	−0.389	−0.255

Note: Significance levels are not provided because the same taxa were originally used to generate the axes.
[a]These entries represent the three most extreme positive and the three most extreme negative correlations with each axis.

observed habitat-related differences among the sites (Table 1). For example, site 5 was characterized by silt covered with detritus and woody debris, whereas site 2 was composed of rocks and boulders. In contrast, the predominant substrates at sites 1, 3, and 4 were sand or silt with macrophytes. The similarities in the benthic community from these latter three sites are evident by the overlap among the replicate samples on CA1 and CA2.

The temporal SDs on the three CA axes for Harp Lake were much larger than those obtained for the samples collected on the same day from Pincher Lake (Table 3). However, the temporal SDs were still smaller than the spatial SDs, suggesting that spatial differences among the sites predominated at a 3-week sampling period. The reduced precision (i.e., larger temporal SDs) in estimating trends in the overall benthic community are highlighted in the CA ordination (Fig. 4) where the weekly samples for a given site are not clustered together like the samples collected on the same day (Fig. 3).

Samples collected every 6–10 weeks

Of the major taxonomic groups collected from Blue Chalk Lake over the ice-free season, 12 groups were infrequently encountered, whereas 13 were routinely collected in large numbers (particularly the dipterans, see Table 2). Results of the two-way ANOVA contrasting spatial and temporal effects revealed that temporal variation predominated (Fig. 2*c*). The proportion of the total variance explained by the ANOVA ranged from 0 to 80%, with an average of 36.2%. Only five taxa were classified as being reliably enumerated at this 6-week time frame using the criterion of at least 50% of the total variance explained by the two-way ANOVA. These five taxa were Ephemeroptera (6), Ceratopogonidae (13), Tanypodinae (15), Chironomini (19), and Gastropoda (21). Of these five taxonomic groups, temporal variance components exceeded spatial variance components for all but the Ceratopogonidae; thus, only the Ceratopogonidae provided results with high repeatability. Spatial effects, which accounted for an average of 60.4 and 46.1% for the same-day and weekly sampling periods, respectively, dropped to an average of 9.4%. By contrast, the temporal variance component increased from 2 and 6%, respectively, to an average of 25.6%, emphasizing that the repeatabilities for most taxa decreased as the sampling period was lengthened.

The total variance explained by the two-way ANOVA dropped from over 70% for the same-day samples to less than 10% for the Oligochaeta (2), and to approximately 30% for the Amphipoda (4), Odonata (7), Coleoptera (11), total Diptera (12), Chironomidae (14), and Tanytarsini (20) (Fig. 2*c*). The proportion of the total variance explained increased from 0 to 80% for Ephemeroptera (6), and from 7 to 34% for Orthocladiinae (17). Spatial effects exceeded temporal effects in the collections of Ceratopogonidae (13), Chironominae (18), and Tanytarsini (20). Temporal effects predominated in the catches of Ephemeroptera (6), Trichoptera (9), Coleoptera (11), Orthocladiinae (17), and Pelecypoda (22).

Given that temporal effects predominated in the two-way ANOVA, the CVs provide a comparative measure of the relative precision of the kick-and-sweep sampling over the ice-free season (Table 3). Here, relative precision includes seasonal variation with sampling and sample processing error. For example, temporal CVs for the Amphipoda and the total Diptera were the smallest, whereas the largest CVs were associated with the Gastropoda (169%), Ephemeroptera (117%), and Nematoda (104%). However, the temporal CVs were all larger than 30%, suggesting relatively poor precision in abundance estimates on the basis of samples collected every 6 weeks. This poor precision is

further illustrated by the fact that the temporal CVs were very similar to the spatial CVs.

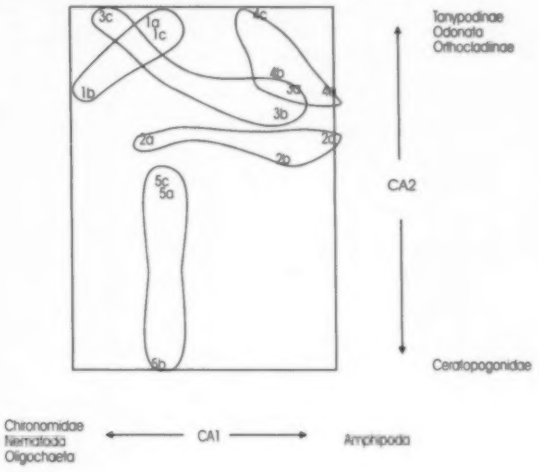
The first three axes from the CA ordination summarized 72% of the total variation (chi-square = 3227.9 with 247 df, $P < 0.001$). CA1 incorporated 35% of the variation, whereas CA2 and CA3 accounted for 23 and 14% of the variation, respectively. A two-way ANOVA using each of these three axes revealed that temporal (including seasonal) variation accounted for the largest proportion of the explained variance in the site scores. By contrast, the spatial variance components dropped to less than 10% of the variance on each axis. The ANOVA significantly separated means on CA2 ($F = 3.68$, $P = 0.023$), but not along CA1 ($F = 2.73$, $P = 0.061$) or CA3 ($F = 1.79$, $P = 0.179$). These trends are illustrated by the fact that polygons enclosing samples collected on the same date exhibited only modest overlap on the first two ordination axes (Fig. 5). Samples collected in September were distinguished from the other three periods along CA1 by greater abundances of Odonata, Trichoptera, and Pelecypoda and lower abundances of Tanypodinae, Ephemeroptera, and Chironominae (Table 6). The May and November samples were separated from the June and September samples on CA2 by lower abundances of Gastropoda, Orthocladiinae, and Oligochaeta, and greater numbers of Ephemeroptera. Seasonal differences predominated despite differences in the substrates at the five sites in Blue Chalk Lake. For example, sites 1 and 5 were characterized by silt and sand with macrophytes, site 2 had rock and gravel substrate, whereas the sediments at sites 3 and 4 were generally comprised of silt and detritus (Table 1). The increase in variance attributed to temporal factors reflects a decrease in the importance of habitat-related differences among the sites when sampling spans larger time periods.

The increased importance of temporal variation is also illustrated by the SDs calculated from the CA scores (Table 3). For samples collected on the same day the temporal SDs were much smaller than the spatial SDs. When samples were collected over a 3-week period, the temporal SDs were still less than the spatial SDs. However, the temporal SDs were larger than the spatial SDs among samples collected every 6 weeks. This loss of spatial resolution is best illustrated by comparing the three ordinations where samples collected every 6 weeks tended to cluster by date rather than by site (Fig. 5).

Discussion

Renewed interest in community stability (e.g., Pimm 1984) has raised questions concerning the best method to examine stability, or its complement, variability (Grossman et al. 1990; Rahel 1990). Resh and Rosenberg (1989) found that spatial and temporal variability are rarely considered in the same study, and often within-sample variation is ignored by approaches that compare means rather than individual observations. Resh and Rosenberg (1989) recommended that an analysis of variability should involve a method that assesses the relative importance of a hierarchical series of spatial and temporal factors. Pollard and Peck (1991) proposed that model II ANOVA will serve this purpose by quantitatively estimating the spatial and temporal

Fig. 4. Plot of the site scores for the first two axes from the correspondence analysis of the Harp Lake data collected in 3 consecutive weeks. Polygons surround samples from the same site highlighting the predominant site (spatial) effects revealed by the ANOVA.



variance components associated with a particular sampling design. This approach differs from traditional (model I) ANOVA, where the emphasis is placed on identifying significant differences among a series of means (e.g., Mackey et al. 1984; Kerans et al. 1992).

Lewis (1978) and Threlkeld (1983) used variance components to examine the relative importance of spatial and temporal factors in the study of zooplankton communities. Similarly, Matthews (1990) and Meador and Matthews (1991) used this approach to assess the stability of fish communities in streams. However, Pollard and Peck (1991) noted that variance components should also be used as a routine QA/QC method to evaluate the quality of data. This latter application focuses on the repeatability of sample means and is particularly important in studies addressing issues of water-quality impairment or ecosystem health (e.g., Plafkin et al. 1989; Klemm et al. 1990; Gibbons et al. 1993).

We undertook this study to assess the relative importance of spatial and temporal variation in the precision and repeatabiliity of our estimates of the relative abundances of littoral macrobenthos. Repeatability, when measured with variance components, contrasts variation among means with variation within groups (Bailey and Byrnes 1990). If differences among means approach zero, variance components will also approach zero. Thus, repeatability provides insight into our ability to distinguish means, whereas precision only provides a relative measure of the variability about a mean. As a result, precision estimates may be quite different from estimates of repeatability.

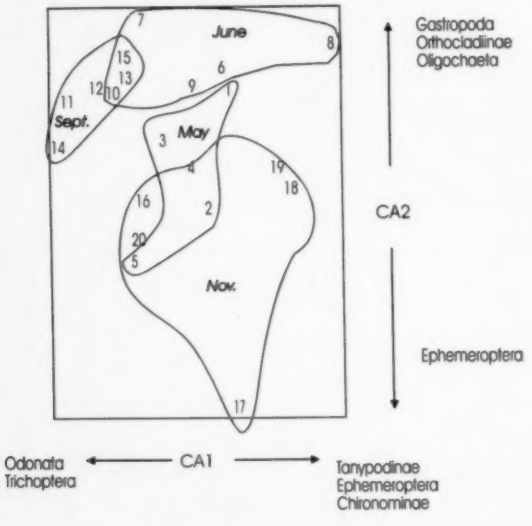
Our analysis of the data from our fixed-time sampling protocol revealed nontrivial spatial and temporal variance components for individual taxonomic groups as well as the multivariate ordination of the benthic community. If fixed-time samples had failed to provide useful quantitative

Table 5. Loadings (correlations) of the abundance of the major taxonomic groups with the first three CA axes on the basis of samples collected over a 3-week period.

	Pearson's correlation			Spearman's correlation		
Taxon	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Nematoda	−0.588[a]	−0.123[a]	−0.424[a]	−0.628[a]	0.009	−0.556[a]
Oligochaeta	−0.582[a]	−0.282[a]	−0.410[a]	−0.574[a]	−0.028[a]	−0.559[a]
Amphipoda	0.472[a]	0.426	0.342	0.427[a]	0.525	0.193[a]
Hydracarina	0.018[a]	0.096	−0.309	0.005[a]	−0.138[a]	−0.409
Ephemeroptera	−0.366	0.208	−0.092	−0.431	0.184	−0.202
Odonata	−0.162	0.479[a]	−0.253	−0.326	0.612[a]	−0.329
Trichoptera	−0.521	0.135	0.514[a]	−0.294	0.044	0.161
Coleoptera	0.117[a]	0.404	0.420[a]	0.112[a]	0.384	0.433[a]
Ceratopogonidae	−0.313	−0.769[a]	0.032	−0.030	−0.525[a]	0.181[a]
Tanypodinae	−0.091	0.447	−0.279	−0.071	0.695[a]	−0.375
Orthocladiinae	−0.407	0.479[a]	−0.380[a]	−0.483	0.574[a]	−0.585[a]
Chironominae	−0.577[a]	0.448[a]	0.104	−0.738[a]	0.501	−0.290
Gastropoda	−0.385	0.236	−0.167	−0.515	0.057	−0.113
Pelecypoda	−0.531	0.110	0.687[a]	−0.497	0.186	0.051

[a]These entries represent the three most extreme positive and the three most extreme negative correlations with each axis.

Fig. 5. Plot of the site scores for the first two axes from the correspondence analysis of the Blue Chalk Lake data. Polygons surround samples collected on the same date (i.e., all five sites) highlighting the predominant date (temporal) effects revealed by the ANOVA.



estimates of relative abundance, we expected that very little of the total variance would be incorporated by the two-way ANOVA or the CA. However, the relative magnitude of temporal variation increased from a minimum for replicate samples collected on the same day, to intermediate values for samples collected weekly, to a maximum for samples collected every 6–10 weeks over the ice-free season (Fig. 2). These results support our predictions. Moreover, these results refute earlier claims that data based on fixed-time sampling are unsuitable for quantitative analyses (Elliott 1977; Pollard 1981; Lenat 1988; France 1992). Our nontrivial results are further supported by the CA ordinations where spatial and temporal clusters of samples were also evident. Thus, we propose that fixed-time sampling protocols can produce quantitative estimates of relative abundance.

From our comparison of variance components and CVs we found that temporal variation was relatively minor among samples collected on the same day. However, temporal variation approached the magnitude of within-lake spatial variation when samples were collected over a 3-week period. Moreover, temporal variation exceeded spatial variation for many taxa as well as the overall community when sampling spanned the ice-free season. This mixing of temporal and spatial variation was evident in all of our major taxonomic groups as well as the patterns in the benthic community based on multivariate ordinations. To maintain temporal variation at a level that is less than within-lake variation, we recommend that sampling should be restricted to a short period of time such as 3 weeks. Longer sampling periods will inadvertently incorporate seasonal differences in abundance that are due to sampling date, not necessarily sampling location.

One of our goals was to identify major taxonomic groups that are sampled with high repeatability and high precision using the timed, kick-and-sweep protocol. Within our ANOVA framework, high repeatability is inferred through the observation of small temporal variance components relative to large within-lake, spatial variance components. Taxa with large temporal variation will have limited utility for distinguishing lakes in multilake faunal surveys that span several weeks to several months. However, taxa exhibiting little or no within-lake variation may assist in

Table 6. Loadings (correlations) of the abundance of the major taxonomic groups on the first three CA axes on the basis of samples collected four times over the ice-free season.

	Pearson's correlation			Spearman's correlation		
Taxon	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Nematoda	−0.159	0.359[a]	−0.506	−0.285	0.203	−0.152
Oligochaeta	−0.271	0.443[a]	−0.596[a]	−0.303	0.308[a]	−0.292[a]
Amphipoda	−0.386[a]	−0.223[a]	0.472[a]	−0.338	−0.215[a]	0.561[a]
Hydracarina	−0.264	0.080	−0.565[a]	−0.234	−0.094	−0.359[a]
Ephemeroptera	0.342	−0.856[a]	0.075	0.566[a]	−0.788[a]	−0.181
Odonata	−0.468[a]	−0.051	0.449[a]	−0.464[a]	−0.113	0.564[a]
Trichoptera	−0.458[a]	−0.057	0.326	−0.375[a]	−0.159	0.421
Coleoptera	−0.287	0.014	−0.143	−0.147	−0.164[a]	−0.254
Ceratopogonidae	−0.015	−0.105[a]	−0.677[a]	0.007	−0.073	−0.621[a]
Tanypodinae	0.859[a]	0.029	0.233	0.848[a]	−0.161	−0.039
Orthocladiinae	0.378[a]	0.296[a]	0.309	0.204	0.348[a]	0.301
Chironominae	0.683[a]	0.105	0.295	0.544[a]	0.199	0.259
Gastropoda	−0.346	0.296[a]	0.376[a]	−0.265	0.543[a]	0.543[a]
Pelecypoda	−0.382	0.295	0.236	−0.365[a]	0.251	0.170

[a]These entries represent the three most extreme positive and the three most extreme negative correlations with each axis.

distinguishing lakes if these taxa are collected with little sampling error or high relative precision. Consequently, taxa with small spatial variance components may also be useful in faunal surveys if these taxa have small temporal CVs.

We found that samples collected on the same day were highly repeatable, with an average temporal variance component of just 2% of the total variation. Exceptions included samples of Hirudinea, Ephemeroptera, and Orthocladiinae (Table 7). Results from the multivariate summary of the benthic community also revealed high repeatability, given that the temporal variance components averaged 0.4% across the first three CA axes. In contrast, within-lake spatial variation dominated the same-day samples by accounting for an average of 60% of the variation among counts of the major taxonomic groups and 55% of the variation in the benthic community. CVs for the same-day samples revealed that collections of Hirudinea, Coleoptera, and Tanypodinae had the least precision, although relative precision for the Ephemeroptera, Trichoptera, and the Pelecypoda was also low. Thus, many taxa were sampled with high repeatability and high precision when sites were resampled on the same day. Counts of Hirudinea and Ephemeroptera were unreliable, whereas counts of Trichoptera and especially Orthocladiinae may also be of limited value.

For samples collected once each week for 3 weeks, spatial variation averaged 46% and temporal variation averaged 6.5%. In addition, the total variation explained by the ANOVA dropped from an average of 62% for samples collected on the same day to 53%. For the benthic community as a whole, spatial variation in the ordination fell from 55 to 32%, whereas temporal variation increased from less than 1 to 5.5%. At this 3-week sampling scale, no variation in the counts of Trichoptera was explained by spatial or temporal factors. In contrast, temporal variance components for Hemiptera, Coleoptera, Hydracarina, and Tanytarsini were large relative to the spatial variance components, and ranged from 19 to 35%. This result suggested that samples of these five taxonomic groups had poor repeatability. In addition, all of the temporal CVs for this 3-week sampling period were larger than 30%, indicating that none of the taxonomic groups was sampled with high precision.

Samples collected every 6 weeks during the ice-free season exhibited considerable temporal variability. For example, the average spatial variance component was 9% whereas the temporal variance averaged 26% and the total variance explained averaged 36%. At this scale, temporal variation exceeded within-lake differences attributed to habitat-related factors. Because of this increased temporal variation and the reduced amount of the total variation explained, we propose that faunal surveys spanning the ice-free season will incorporate considerable temporal variation, thereby blurring differences between lakes with differences associated with sampling date. In contrast, samples collected over a 3-week period incorporate a smaller temporal variance component, suggesting that this short time frame is appropriate to minimize temporal confounding in faunal surveys. However, the generality of this finding should be confirmed because abundances for the April–May, 3-week period used here may be less variable than for similar periods in the mid to late summer.

This study has focused on repeatability and relative precision, which are two aspects of data quality assurance and quality control (QA/QC). Many types of QA/QC procedures are necessary to fully evaluate the biological and statistical significance of benthological surveys (Malley and Reynolds 1979; Barton 1989; Klemm et al. 1990). Our use of repeatability permits an evaluation of the relative importance of temporal and within-lake spatial variation. Similarly, we used CVs to illustrate that sampling precision

Table 7. Summary of the repeatability and precision of the timed, kick-and-sweep sampling protocol.

	Same day, Pincher Lake		3 weeks, Harp Lake		6 weeks, Blue Chalk	
Taxon	Repeatability	Precision	Repeatability	Precision	Repeatability	Precision
Nematoda	—	—	Moderate	Low	Low	Low
Oligochaeta	High	Moderate	High	Low	Low	Low
Hirudinea	Low	Low	—	—	—	—
Amphipoda	High	Moderate	Moderate	Low	Low	Low
Hydracarina	—	—	High	Low	—	—
Ephemeroptera	Low	Low	High	Low	Low	Low
Odonata	High	High	High	Low	Low	Low
Hemiptera	Moderate	High	Moderate	Low	—	—
Trichoptera	Moderate	Low	Low	Low	Low	Low
Coleoptera	High	Low	Low	Low	Low	Low
Diptera						
Total	High	High	High	Moderate	Low	Low
Ceratopogonidae	Moderate	High	Moderate	Low	High	Low
Chironomidae	High	High	High	Moderate	Moderate	Low
Tanypodinae	High	Low	High	Moderate	Low	Low
Prodiamesinae	—	—	Moderate	Low	—	—
Orthocladiinae	Low	Moderate	Moderate	Low	Low	Low
Chironominae	High	High	Moderate	Low	Moderate	Low
Chironomini	High	High	High	Low	Low	Low
Tanytarsini	High	High	High	Low	Moderate	Low
Gastropoda	—	—	Moderate	Low	Low	Low
Pelecypoda	High	Low	High	Low	Low	Low

Note: Repeatability is classified as high (>50% of the variance explained and site effects larger than temporal effects), moderate (>20% of the variance explained and site effects > temporal effects) and low (<20% of the variance explained or site effects < temporal effects); precision is classified as high (CV < 30%), moderate (30% < CV < 40%) or low (CV > 40%) on the basis of temporal CVs.

also drops when the sampling period is increased. Unfortunately, these comparisons lack an estimate of between- or among-lake spatial variation. If we assume that within-lake variation approximates among-lake variation, then a 3-week sampling period only incorporates a modest amount of temporal variation into a multilake survey (cf. France 1992). As a result, our current practice of sampling over a 3-week period each year produces highly repeatable results (e.g., Shaw et al. 1992; Reid et al. 1994*a*, 1994*b*). In contrast, timed kick-and-sweep surveys spanning the ice-free season will inadvertently include temporal variation at a level that exceeds within-lake spatial variation. Future studies will explore the relative importance of substrate characteristics with respect to within-lake and among-lake variation in littoral macroinvertebrate abundance.

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References

Bailey, R.C., and J. Byrnes. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Syst. Zool. 9: 124–130.

Barton, D.R. 1989. Some problems affecting the assessment of Great Lakes water quality using benthic invertebrates. J. Gt. Lakes Res. 15: 611–622.

Bivand, R. 1980. A Monte Carlo study of correlation coefficient estimation with spatially autocorrelated observations. Quaest. Geogr. 6: 5–10.

Clifford, H.F., and R.J. Casey. 1992. Differences between operators in collecting quantitative samples of stream macroinvertebrates. J. Freshwater Ecol. 7: 271–276.

Collins, N.C., A.P. Zimmerman, and R. Knoechel. 1981. Comparisons of benthic infauna and epifauna biomasses in acidified and non-acidified Ontario lakes. p. 35–48. *In* R. Singer [ed.] Effects of acidic precipitation on benthos. Proceedings of a Symposium of the North American Benthological Society, Hamilton, N.Y.

Cuff, W., and N. Coleman. 1979. Optimal survey design: lessons

from a stratified random sample of macrobenthos. J. Fish. Res. Board Can. 36: 351–361.

Davis, N., and G.R. van Blaricom. 1978. Spatial and temporal heterogeneity in a sand bottom epifaunal community of invertebrates in shallow water. Limnol. Oceanogr. 23: 417–427.

Dermott, R., J.R.M. Kelso, and A. Douglas. 1986. The benthic fauna of 41 acid sensitive headwater lakes in north central Ontario. Water Air Soil Pollut. 28: 283–292.

Dillon, P.J., R.A. Reid, and E. de Grosbois. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. Nature (London), 329: 45–48.

Doledec, S., and D. Chessel. 1991. Recent developments in linear ordination methods for environmental sciences. Adv. Ecol. 1: 133–155.

Downing, J.A., and H. Cyr. 1985. Quantitative estimation of epiphytic invertebrate populations. Can. J. Fish. Aquat. Sci. 42: 1570–1579.

Downing, J.A., and W.L. Downing. 1992. Spatial aggregation, precision and power in surveys of freshwater mussel populations. Can. J. Fish. Aquat. Sci. 49: 985–991.

Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. 2nd ed. Freshwater Biol. Assoc. Sci. Publ. No. 25. The Ferry House, Ambleside, Cumbria.

Ezcurra, E. 1987. A comparison of reciprocal averaging and non-centred principal components analysis. Vegetatio, 71: 41–47.

Ettinger, W. 1984. Variation between technicians sorting benthic macroinvertebrate samples. Freshwat. Invertebr. Biol. 3: 147–149.

France, R.L. 1990. Theoretical framework for developing and operationalizing an index of zoobenthos community integrity: application to biomonitoring with zoobenthos communities in the Great Lakes. p. 169–193. *In* C.J. Edwards and H.A. Regier [ed.] An ecosystem approach to the integrity of the Great Lakes in turbulent times. Gt. Lakes Fish. Comm. Spec. Publ. 90-4.

France, R.L. 1992. Use of sequential sampling of amphipod abundance to classify the biotic integrity of acid-sensitive lakes. Environ. Manage. 16: 157–166.

Furse, M.T., J.F. Wright, P.D. Armitage, and D. Moss. 1981. An appraisal of pond-net samples for biological monitoring of lotic macro-invertebrates. Water Res. 15: 679–689.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Gauch, H.G., R.H. Whittaker, and T.R. Wentworth. 1977. A comparative study of reciprocal averaging and other ordination techniques. J. Ecol. 65: 157–174.

Gibbons, W.D., M.D. Munn, and M.D. Paine. 1993. Guidelines for monitoring benthos in freshwater environments. Report for Environment Canada, North Vancouver, B.C., prepared by EVS Consultants.

Grossman, G.D., J.F. Dowd, and M. Crawford. 1990. Assemblage stability in stream fishes: a review. Environ. Manage. 14: 661–671.

Harman, W.N. 1974. Snails (Mollusca: Gastropoda). p. 275–312. *In* C.W. Hart, Jr., and S.L.H. Fuller [ed.] Pollution ecology of freshwater invertebrates. Academic Press, New York.

Harvey, H.H., and J.M. McArdle. 1986. Composition of the benthos in relation to pH in the LaCloche lakes. Water Air Soil Pollut. 30: 529–536.

Hill, M.O. 1974. Correspondence analysis: a neglected multivariate method. Appl. Stat. 23: 340–354.

Hilsenhoff, W.L. 1988. Rapid field assessment of organic pollution with a family-level biotic index. J. North Am. Benthol. Soc. 7: 65–68.

Jancey, R.C. 1979. Species ordering on a variance criterion. Vegetatio, 39: 59–63.

Kerans, B.L., J.R. Karr, and S.A. Ahlstedt. 1992. Aquatic invertebrate assemblages: spatial and temporal differences among sampling protocols. J. North Am. Benthol. Soc. 11: 377–390.

Klemm, D.J., P.A. Lewis, F. Fulk, and J.M. Lazorchak. 1990. Macroinvertebrate field and laboratory methods for evaluating the biological integrity of surface waters. U.S. Environ. Prot. Agency Res. Dev. Rep. EPA/600/4-90/030.

Krebs, C.J. 1989. Ecological methodology. Harper and Row, Publishers, New York.

Lauritsen, D.D., S.C. Mozley, and D.S. White. 1985. Distribution of oligochaetes in Lake Michigan and comments on their use as indices of pollution. J. Gt. Lakes Res. 11: 67–76.

Lenat, D.R. 1988. Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. J. North Am. Benthol. Soc. 7: 222–233.

Lewis, W.M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology, 59: 666–671.

Mackey, A.P., D.A. Cooling, and A.D. Berrie. 1984. An evaluation of sampling strategies for qualitative surveys of macro-invertebrates in rivers, using pond nets. J. Appl. Ecol. 21: 515–534.

Mackie, G.L. 1989. Tolerances of five benthic invertebrates to hydrogen ions and metals (Cd, Pb, Al). Arch. Environ. Contam. Toxicol. 18: 215–223.

Malley, D.F., and J.B. Reynolds. 1979. Sampling strategies and life history of non-insectan freshwater invertebrates. J. Fish. Res. Board Can. 36: 311–318.

Matthews, W.J. 1990. Spatial and temporal variation in fishes of riffle habitats: a comparison of analytical approaches for the Roanoke River. Am. Midl. Nat. 124: 31–45.

McAuliffe, J.R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. Ecology, 65: 894–908.

Meador, M.R., and W.J. Matthews. 1991. Spatial and temporal patterns in fish assemblage structure of an intermittent Texas stream. Am. Midl. Nat. 127: 106–114.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio, 69: 89–107.

Morin, A., and A. Cattaneo. 1992. Factors affecting sampling variability of freshwater periphyton and the power of periphyton studies. Can. J. Fish. Aquat. Sci. 49: 1695–1703.

Nalepa, T.F., and N.A. Thomas. 1976. Distribution of macrobenthic species in Lake Ontario in relation to sources of pollution and sediment parameters. J. Gt. Lakes Res. 2: 150–163.

Okland, J., and K.A. Okland. 1979. Use of fresh-water littoral fauna for environmental monitoring: aspects related to studies of 1000 lakes in Norway. p. 168–183. *In* H. Hytteborn [ed.] The use of ecological variables in environmental monitoring. Nat. Swed. Environ. Prot. Board Rep. No. SNV PM 1151.

Okland, J., and K.A. Okland. 1986. The effects of acid deposition on benthic animals in lakes and streams. Experientia, 42: 471–486.

Oksanen, J. 1983. Ordination of boreal heath-like vegetation with principal component analysis, correspondence analysis and multidimensional scaling. Vegetatio, 52: 181–189.

Orloci, L. 1975. Measurement of redundancy in species collections. Vegetatio, 31: 65–67.

Peterson, C.H. 1975. Stability of species and of community for the benthos of two lagoons. Ecology, 56: 958–965.

Pimm, S.L. 1984. The complexity and stability of ecosystems. Nature (London), 307: 321–326.

Plafkin, J.L., M.T. Barbour, K.D. Porter, S.K. Gross, and R.M. Hughes. 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. EPA/440/4-89/001.

Pollard, J.E. 1981. Investigator differences associated with a kicking method for sampling macroinvertebrates. J. Freshwater Ecol. 1: 215–224.

Pollard, J.E., and D.V. Peck. 1991. Biological quality assurance for ecological monitoring: can we use chemistry as a template? p. 43–53. *In* D.R. Hart [ed.] Proceedings of the Third Annual Ecological Quality Assurance Workshop, Burlington, Ont.

Poulton, D.J., K.J. Simpson, D.R. Barton, and K.R. Lum. 1988. Trace metals and benthic invertebrates in sediments of nearshore Lake Ontario at Hamilton Harbour. J. Gt. Lakes Res. 14: 52–65.

Rabeni, C.F., S.P. Davies, and K.E. Gibbs. 1985. Benthic invertebrate response to pollution abatement: structural changes and functional implications. Wat. Resour. Bull. 21: 489–497.

Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. Am. Nat. 136: 328–344.

Reid, R.A., S.M. David, and R.E. Girard. 1994*a*. The littoral-zone benthic macroinvertebrate communities of 12 acid-sensitive, headwater lakes in south-central Ontario: lake selection and preliminary sampling results. Tech. Rep. Ontario Ministry of the Environment and Energy, Toronto, Ont.

Reid, R.A., S.M. David, and R.E. Girard. 1994*b*. The littoral-zone benthic macroinvertebrate communities of 12 acid-sensitive, headwater lakes in south-central Ontario: a comparison of spring and fall collections. Tech. Rep. Ontario Ministry of the Environment and Energy, Toronto, Ont.

Resh, V.H., and D.M. Rosenberg. 1989. Spatial-temporal variability and the study of aquatic insects. Can. Entomol. 121: 941–963.

Roback, S.S. 1974. Insects (Arthropoda: Insecta). p. 313–376. *In* C.W. Hart, Jr., and S.L.H. Fuller [ed.] Pollution ecology of freshwater invertebrates. Academic Press, New York.

Roff, J.C., and R.E. Kwiatkowski. 1977. Zooplankton and zoobenthos communities of selected northern Ontario lakes of different acidities. Can. J. Zool. 55: 899–911.

Rohlf, F.J. 1988. NTSYS-pc numerical taxonomy and multivariate analysis system. Version 1.50. Exeter Publishing Ltd., Setauket, N.Y.

SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

Shaw, M.A., S. Geiling, S. Barbour, I.J. Davies, E.A. Hamilton, A. Kemp, R. Reid, P.M. Ryan, N. Watson, and W. White. 1992. The Department of Fisheries and Oceans National LRTAP biomonitoring programme: site locations, physical and chemical characteristics. Can. Tech. Rep. Fish. Aquat. Sci. No. 1875.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W.H. Freeman and Co., New York.

Stephenson, M., and G.L. Mackie. 1986. Lake acidification as a limiting factor in the distribution of the freshwater amphipod *Hyalella azteca*. Can. J. Fish. Aquat. Sci. 43: 288–292.

Stephenson, M., G. Mierle, R.A. Reid, and G.L. Mackie. 1994. Effects of experimental and cultural lake acidification on littoral benthic macroinvertebrate assemblages. Can. J. Fish. Aquat. Sci. 51: 1147–1161.

ter Braak, C.J.F., and I.C. Prentice. 1988. A theory of gradient analysis. Adv. Ecol. Res. 18: 271–317.

Threlkeld, S.T. 1983. Spatial and temporal variation in the summer zooplankton community of a riverine reservoir. Hydrobiologia, 107: 249–254.

Warwick, R.M. 1988. Analysis of community attributes of the macrobenthos of Frierfjord/Langesundifjord at taxonomic levels higher than species. Mar. Ecol. Prog. Ser. 46: 167–170.

Warwick, R.M., and K.R. Clarke. 1991. A comparsion of some methods for analyzing changes in benthic community structure. J. Mar. Biol. Assoc. U.K. 71: 225–244.

Wilhm, J.L., and T.C. Dorris. 1968. Biological parameters for water quality criteria. Bioscience, 18: 477–481.

Wright, J.F. 1992. Spatial and temporal occurrence of invertebrates in a chalk stream, Berkshire, England. Hydrobiologia, 248: 11–30.

Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS

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Abstract: Retrospective determination of the early life history of fish using the microelemental analysis of their otoliths is dependent upon understanding the factors that affect this elemental composition. Here, juvenile Atlantic croaker (*Micropogonias undulatus*) were reared under different treatments of temperature and salinity to determine their impacts on elemental inclusion rates in otoliths. Solution-based inductively coupled plasma mass spectrometry (ICPMS) was used to measure 21 isotopes in each otolith: isotopic concentrations ranged over seven orders of magnitude, and differed significantly amongst the temperature–salinity regimes. Univariate analyses identified 13 isotopes that contributed to these multivariate differences; the influence of temperature was stronger than that of salinity. Within each treatment there was a significant relationship between otolith microchemistry and otolith size. To some extent this confounded the interpretation of the between-treatment effect of temperature. In contrast, both the otolith and somatic growth rates were similar between the two salinity treatments, indicating that differences in elemental fingerprints were unambiguously related to the salinity difference, probably a response to the elemental concentrations in the tank water. Overall the study highlighted the current poor understanding of the mechanism of contamination of otoliths by trace elements and their incorporation into the otolith microstructure.

Résumé : La reconstitution du début du cycle biologique d'un poisson à l'aie de l'analyse des micro-éléments présents dans ses otolithes est tributaire de la compréhension des facteurs qui agissent sur la composition élémentaire de ces organes. Nous avons élevé dans diverses conditions de température et de salinité des juvéniles de tambour brésilien (*Micropogonias undulatus*) pour mesurer les effets de ces traitements sur le taux d'absorption des éléments dans les otolithes. La spectrométrie de masse avec plasma inductif en solution a permis de mesurer la concentration de 21 isotopes dans chaque otolithe; ces concentrations couvraient sept ordres de grandeur et différaient de façon significative selon les régimes de température et de salinité. Des analyses univariées ont permis de repérer 13 isotopes contribuant à ces différences dans l'analyse à plusieurs variables; l'influence de la température était plus forte que celle de la salinité. Pour chaque traitement, on observait une relation significative entre la microchimie de l'otolithe et sa taille, ce qui créait une certaine confusion dans l'interprétation de l'effet des divers régimes de température. Par contre, le taux de croissance des otolithes et celui de l'ensemble du corps étaient à peu près les mêmes pour les deux conditions de salinité, ce qui indique que les différences dans les empreintes des éléments liées, sans ambiguïté possible, à la différence de salinité; il s'agit probablement d'une réaction aux concentrations des éléments dans l'eau de l'aquarium. Dans l'ensemble, l'étude a mis en relief les carences qui subsistent dans la compréhension du mécanisme de contamination des otolithes par les éléments traces et de leur absorption par la microstructure des otolithes.

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Introduction

Otoliths of teleost fishes are small, calcareous structures located within the inner ear, whose primary function appears to be the detection of sound. These structures have also become valuable research tools for fish biologists, now being the preferred structure for use in large-scale direct ageing studies based on the enumeration of annuli (Pentilla and Dery 1988; Beamish 1992). Furthermore, their microstructure provides an accurate chronology of growth and life-history transitions, which has revolutionized studies of early life history (Campana and Neilson 1985; Jones 1986; Jones 1992). Recently, a significant new research priority has developed based on otoliths. Their elemental composition ("microchemistry") is being used increasingly to retrospectively describe the life history of fish, in particular to identify the environments they have experienced (reviewed Gunn et al. 1992; Radtke and Shafer 1992; Secor et al. 1994).

The use of otoliths as environmental recorders is based on the premise that the differences in water chemistry amongst different aquatic environments are manifested in the elemental composition of otoliths (Radtke and Shafer 1992; Campana and Gagne 1994). It is also dependent on the observation that otoliths are acellular and physiologically static; once accreted, material is not resorbed or metabolically reworked (Campana and Neilson 1985). Already otolith microchemistry has proved to be a useful tool, having been used to determine the age of fish (Bennett et al. 1982; Campana et al. 1990), to distinguish amongst their stocks (Edmonds et al. 1989, 1991, 1992; Campana and Gagne 1994; Campana et al. 1994), and to describe the environmental conditions experienced at various life-history stages (e.g. Radtke 1984; Kalish 1990, 1991*b*; Secor 1992; Radtke and Shafer 1992).

Interpretation of the life-history information that has been chemically encoded within the otolith can only be achieved after the elemental composition has been determined. One of the most powerful procedures now available to achieve this is inductively coupled plasma mass spectrometry (ICPMS). Since its first commercial application in 1983, its multielement capabilities, broad linear range, and its ability to discriminate amongst isotopes made ICPMS a significant tool for use in the earth sciences (Date 1991; Jarvis and Jarvis 1992). ICPMS can be used to analyse otoliths in two ways: solution-based ICPMS for the analysis of whole otoliths, and laser ablation ICPMS (LA-ICPMS) for sampling specific loci within otoliths. To date, the former has been applied to the elemental analysis of whole otoliths from adult fish (Edmonds et al. 1992; Campana and Gagne 1994), in each case successfully discriminating amongst fish collected from different places. Laser ablation ICPMS has recently been successfully applied to the assay of the elemental composition of nuclei in otoliths of adult cod (Campana et al. 1994), also successfully discriminating amongst fish collected from different places.

Application of microelemental analysis to field studies depends on the ability to accurately interpret such analyses. The aim of this project was to improve our understanding of the factors that affect the microchemistry of the otoliths of juvenile Atlantic croaker (*Micropogonias undulatus*), to facilitate its use for understanding the life history of wild fish. Consequently, fish were reared under constant conditions at different temperatures and salinities to assess their effect on otolith microchemistry. The present paper is concerned with the analysis of otoliths by solution-based ICPMS, whilst the following paper reports the results of analyses from the same fish using LA-ICPMS (Fowler et al. 1995). The specific aims here were to (1) identify the elements that occur in the otoliths of Atlantic croaker; (2) determine their absolute concentrations; and (3) determine whether the rate of incorporation varies under different environmental conditions.

Materials and methods

Juvenile Atlantic croaker used in this experiment were reared at the National Marine Fisheries Service (NMFS) Laboratory, Beaufort, N.C. Adult fish were induced to spawn through temperature manipulation and injection. Eggs were reared for the first 24 h in a common tank (22°C and 33‰ salinity) and then transferred to eight separate 100-L rearing tanks, with an initial stocking density of 500 eggs per tank. Each tank was supplied with water from the same initial source, with treatments established by diluting with deionized water and (or) heating. The four treatments assigned randomly to two tanks each were as follows treatment 1, 20°C and 26‰ salinity; treatment 2, 20°C and 35‰ salinity; treatment 3, 25°C and 26‰ salinity; treatment 4, 25°C and 35‰ salinity.

After hatching, the larvae were fed ad libitum with rotifers, whose concentration in the tanks was always kept in excess of consumption. A 12 h dark : 12 h light diurnal cycle was maintained. Oxygen was always kept at saturation in each tank using aerators. All tanks were maintained for 71 days from 28 October 1992 (day 1) until 6 January 1993 (day 71), after which the surviving fish were killed, measured (standard and total length), and frozen in individual acid-washed glass vials.

A number of fish were removed from each tank at different times throughout the rearing period for a separate study to determine the periodicity of increment formation in otoliths. Furthermore, there was considerable variation in the survivorship amongst the treatments and tanks. Unfortunately, the total loss of fish from both tanks of treatment 4 eliminated the high temperature – high salinity treatment (25°C and 35‰ salinity), whilst one tank was lost from treatment 2 (20°C and 35‰ salinity). Fish that died prior to the termination date of 6 January were not considered in any subsequent analyses.

General laboratory procedures

To avoid airborne contamination most procedures involving the fish or otoliths were done in a positive flow fume hood, which established a Class 100 clean room. To prevent surface contamination all equipment and plasticware involved in the ICPMS work or otolith storage were acid-washed prior to use. At no stage were fish or otoliths exposed to bare metal.

After the fish were killed, 10 from each tank (except treatment 2 tank 1, $n = 20$), were randomly selected from

Table 1. Details of otolith dissolution prior to solution-based ICPMS.

Treatment	Tank	Fish remaining	Sample size	Mean otolith weight (mg)	Volume of acid (mL)	Volume of H_2O (mL)	Total volume (mL)
1	1	46	10	0.404	0.3	2.7	3.0
(20°C, 26‰)	2	41	10	0.426	0.3	2.9	3.2
2	1	29	20	0.545	0.4	3.7	4.1
(20°C, 35‰)	2	0	—				
3	1	32	10	3.739	2.8	25.0	27.8
(25°C, 26‰)	2	24	10	4.195	3.1	28.1	31.2
4	1	0	—				
(25°C, 35‰)	2	0	—				

Note: Included are the number of fish remaining in each tank at the end of the rearing period, the number of otoliths from each tank analysed by ICPMS, their mean weight, and the volumes of Seastar nitric acid and Super Q water used to dissolve each otolith. All solutions were subsequently diluted twofold.

those available using random number tables. Each fish was dissected using glass probes on a microscope slide using a binocular microscope (ensuring that the otolith or dissection equipment never touched any metal part of the microscope). Both sagittae, one destined for solution-based ICPMS and the other for LA–ICPMS were placed on a clean glass slide, rinsed several times in Super Q water (deionized, purified through reverse osmosis, and millipore filtered), and adhering tissue was removed with the glass probes. These otoliths were then air-dried in the positive flow fume hood. Both air-dried sagittae were weighed (to 0.01mg), and the one destined for solution-based ICPMS was sealed in an acid-washed polyethylene conical vial for acid dissolution.

Solution-based ICPMS

The sagittae were prepared for analysis by dissolution in Seastar brand redistilled nitric acid followed by dilution with Super Q water. It is important to standardize the concentrations of the sample solutions before analysing them with ICPMS (Jarvis and Jarvis 1992), and since the otoliths from fish in the different treatments varied in size, the amounts of acid and water used for otolith dissolution were proportional to the mean weight of the otoliths being dissolved (Table 1). The acid was added to the conical vials first, followed half an hour later by the Super Q water, maintaining a ratio of nine parts water to one part acid (Table 1).

The solution-based ICPMS analyses were done by an external laboratory. The solutions, one from each otolith, were provided to the laboratory in the conical vials in which the otoliths had been dissolved. Each solution was then further diluted twofold prior to assay. Our samples were all analysed on a single day in five blocks. The samples from the five tanks were divided evenly amongst the five blocks, and their within-block order was random. Prior to analyses the ICPMS was calibrated with standards and thereafter let to drift. In the subsequent data analyses, sequence number was used as a covariate to statistically remove this instrument-drift influence.

Data analysis

Results from solution-based ICPMS were expressed in terms of solution concentration (micrograms per litre) for each isotope within each otolith. Isotopic concentrations were converted to elemental concentrations based on percent natural abundances, and then converted to parts per million, based on otolith weight and the total volumes used for dissolution (Table 1). Elemental concentrations were analysed using a combination of multivariate and univariate techniques. Prior to analysis all variables were transformed ($y = \log_e x$), to stabilize variance–covariance matrices in the multivariate tests, and to ensure homogeneity of variances and normality of residuals in univariate analyses.

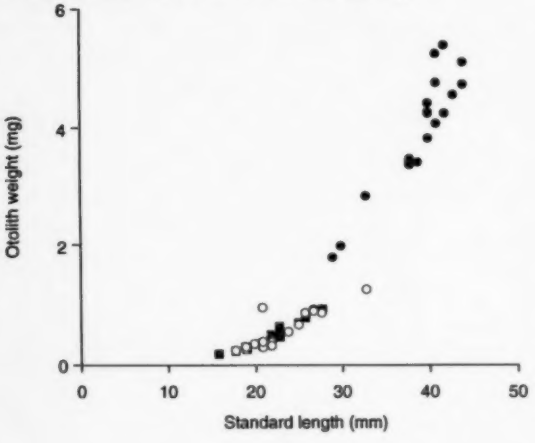
Elemental compositions of otoliths were analysed by multivariate analysis of covariance. Treatment was considered a fixed effect in the design, and sequence number was introduced to the model as a covariate to account for instrument drift. The multivariate analysis of covariance (MANCOVA) was followed by a canonical discriminant analysis (CDA) to identify where differences among treatments occurred. Before the CDA analysis, the effect of sequence was removed from each of the isotopes using the pooled within-groups slope. Finally, a factor analysis was done to identify the isotopes that were loading together in the multivariate analyses.

Univariate analyses were used to identify individual isotopes contributing to the differences detected in the MANCOVA and CDA analyses. The data for each isotope were analysed using ANOVA, with tanks nested within treatments. To allow a more powerful test of the treatment effect, data were pooled across tanks when the tank effect was not significant at $p > 0.2$. An alpha level of 0.05 was used here despite the number of comparisons being made, as we were using such analyses as indicators of those

Table 2. Details of the size of fish and otoliths that were considered in the microelemental analyses by ICPMS. In each case the mean (±SD) is given.

Treatment	Tank	Mean standard length (mm)	Mean otolith weight (mg)	Mean otolith length length (mm)
1	1	21.1±3.5	0.40±0.24	1.22±0.27
(20°C, 26‰)	2	22.3±3.5	0.43±0.17	1.29±0.23
2	1	23.1±3.8	0.55±0.31	1.34±0.24
(20°C, 35‰)	2	—	—	—
3	1	36.3±4.3	3.74±1.17	2.48±0.31
(25°C, 26‰)	2	38.7±2.4	4.20±0.73	2.63±0.16
4	1	—	—	—
(25°C, 35‰)	2	—	—	—

Fig. 1. Relationship between otolith weight and standard length for fish from the three surviving treatments. Open circles relate to treatment 1, 20°C and 26‰ salinity; solid squares to treatment 2, 20°C and 35‰ salinity; and solid circles to treatment 3, 25°C and 26‰ salinity.



isotopes likely to have contributed to the multivariate differences identified by the MANCOVA. When an ANOVA was significant, means were compared using Tukey's honestly significant difference, applying Kramer's correction for unequal sample sizes (Quinn and Day 1989).

Results

Fish and otolith growth

The fish that had been maintained at low temperatures were much smaller than those from the higher temperature regime, a difference that was also reflected in the otolith weights and lengths (Table 2). Fish from the low-temperature tanks had otoliths approximately half the length and one tenth the weight of those from fish reared at higher temperatures (Table 2). Consideration of the otolith weight and fish size relationships (Fig. 1) suggested that the high-temperature treatment caused a higher rate of increase in otolith weight relative to standard length, than the low-temperature treatments. There was no apparent effect of salinity here.

Solution-based ICPMS

A total of 21 isotopes representing 16 elements was detected in the otolith solutions. Initial plots for some isotopes against sequence number displayed significant trends related to instrument drift, particularly evident for some major elements such as Ca. Furthermore, in some cases, different isotopes from the same element drifted in different directions. Consequently, sequence number was treated as a covariate and removed from the analyses. The concentrations of the 16 elements calculated from the isotopic concentrations of the 21 isotopes ranged over seven orders of magnitude (Table 3). Calcium dominated the results followed by chlorine and strontium (Table 3). Iron and phosphorus were present in hundreds of parts per million, whilst the remaining elements were at less than 100 ppm. Differences in elemental concentrations from isotopes of the same element are related to different rates of interference from other ions and variation in counting.

The multivariate analysis of variance indicated a significant difference in the elemental fingerprints of otoliths from the three treatments (Pillai's Trace = 1.446, $F = 4.83$, df = 40, 74, $p < 0.0001$), along with a significant effect of the sequence covariate. The canonical discriminant analysis that relates the results from the three treatments to each other indicates a clear separation amongst them (Fig. 2). The isolation of treatment 3 from the other two along canonical variate 1 is coincident with the difference in temperature regimes. The separation between treatments 1 and 2 along canonical variate 2 reflects the effect of salinity on otolith microchemistry. Factor analysis was then used to look for affinities amongst the 21 isotopes. The calcium and strontium isotopes, along with ^{57}Fe, separated from all others along factor 1 (Fig. 3). Each of these had higher concentrations within treatment 3 than treatments 1 and 2, suggesting that their separation could be related to temperature (Table 3). Calcium and strontium isotopes separated from ^{26}Mg, ^{55}Mn, ^{31}P, and ^{85}Rb along factor 2, probably due to salinity.

There was a significant difference in the elemental composition of otoliths from the three treatments (Fig. 2). However, the cause of this is ambiguous as the treatment effect also resulted in differences in growth rate; treatment 3 (high temperature) produced large otoliths and treatments 1 and 2 (low temperature) small otoliths (Table 2). We used principal components analysis (PCA) to assess the influence of growth on otolith composition. Linear combinations of the data for all 21 isotopes were constructed using PCA. The first principal component, accounting for 37.2% of the variability within the matrix, was graphed against otolith weight (Fig. 4). For each treatment there was a monotonic decreasing function between the first principal component and otolith weight, indicating

Table 3. Summary of concentrations of the 21 isotopes that were significantly above background levels in the otoliths of fish from each tank.

	Treatment 1 (ppm)				Treatment 2 (ppm)		Treatment 3 (ppm)			
	Tank 1		Tank 2		Tank 1		Tank 1		Tank 2	
Isotope	Median	Range	Median	Range	Median	Range	Median	Range	Median	Range
^{7}Li	1.2	0.8	1.2	0.5	1.7	1.4	0.9	0.3	1.3	0.4
^{26}Mg	144.3	50.2	135.5	41.2	122.6	81.8	69.2	26.3	72.3	23.4
^{27}Al	44.1	47.6	50.3	35.7	24.6	22.2	28.3	27.5	26.8	12.2
^{31}P	790.4	545.5	853.6	141.8	874.5	589.5	256.5	113.2	274.3	58.5
^{35}Cl	10 479.6	11 624.2	10 788.6	2 590.5	11 181.8	11 999.7	12 277.6	3 916.2	11 675.6	3 269.8
^{44}Ca	467 974.0	41 855.0	454 170.0	47 907.0	478 058.0	59 060.0	502 815.0	81 915.0	485 423.0	65 100.0
^{48}Ca	338 832.0	24 905.0	330 000.0	37 992.0	335 016.0	14 310.0	363 474.0	12 482.0	365 705.0	8 427.0
^{55}Mn	7.2	1.3	7.2	1.5	7.3	2.7	4.6	0.8	5.8	1.2
^{57}Fe	358.0	128.1	344.9	64.2	362.4	49.7	354.8	38.9	362.4	49.7
^{60}Ni	11.0	12.5	5.0	1.6	5.8	5.3	5.3	3.8	4.9	2.5
^{65}Cu	4.4	1.6	4.7	2.1	3.3	3.2	2.4	1.9	2.7	1.1
^{66}Zn	82.9	50.0	59.7	29.0	54.6	92.1	25.3	54.3	37.2	20.4
^{68}Zn	78.5	51.8	58.6	23.2	54.0	86.9	23.6	46.5	37.9	13.3
^{75}As	0.4	0.2	0.7	0.4	0.6	0.5	0.6	0.3	0.5	0.5
^{85}Rb	0.6	0.7	0.8	0.5	0.6	0.4	0.4	0.2	0.5	0.2
^{86}Sr	1 421.8	229.0	1 350.4	130.9	1 378.4	206.4	1 660.4	216.0	1 804.0	190.5
^{87}Sr	1 378.9	232.8	1 248.8	132.6	1 364.6	226.2	1 640.7	227.8	1 767.0	221.0
^{88}Sr	2 013.1	213.5	1 899.6	114.2	1 929.0	174.1	2 330.1	213.6	2 528.1	376.5
^{137}Ba	5.8	2.4	4.3	5.8	5.3	4.2	5.9	2.9	6.0	9.8
^{138}Ba	5.0	2.7	4.1	6.3	4.5	3.8	5.3	2.6	5.6	10.6
^{208}Pb	2.1	2.6	1.6	1.4	1.3	2.0	0.7	1.7	1.7	2.5

Note: Sample size is 10 except treatment 2, tank 1, where $n = 20$. (Treatment 1, 20°C and 26‰; treatment 2, 20°C and 35‰; treatment 3, 25°C and 35‰.)

that within a given treatment, elemental composition is a function of otolith size and growth rate.

Individual isotopes were analysed independently to identify those contributing to the separation among treatments. No isotope demonstrated a significant tank effect; indeed, p was less than 0.2 for only two isotopes, ^{7}Li and ^{60}Ni (Table 4). Thirteen isotopes demonstrated a significant difference amongst treatments (Table 4, Fig. 5). In most cases the mean for treatment 3 was significantly different from those for treatments 1 and 2, reflecting an effect of temperature. For ^{26}Mg, ^{31}P, ^{55}Mn, ^{65}Cu, ^{66}Zn, and ^{68}Zn this mean was significantly lower whilst for ^{44}Ca, ^{48}Ca, ^{57}Fe, and the three Sr isotopes the mean for treatment 3 was higher. For ^{44}Ca a significant difference between treatments 1 and 2 indicated an effect of salinity.

Discussion

The use of microelemental analysis of otoliths to address questions about the early life history of fish depends on interpreting the elemental fingerprints to identify residence times within water masses of different chemistries. Yet, elemental fingerprints from otoliths may not be a simple reflection of the elemental composition of the seawater, since numerous other factors may influence the rates at which ions are deposited in otoliths (Kalish 1989, 1991*a*; Radtke and Shafer 1992). By rearing juvenile Atlantic croaker under controlled environmental conditions we were able to assess the effect of water temperature and salinity on otolith microchemistry, whilst simultaneously minimizing the effect of other potentially confounding influences.

Factors affecting otolith microchemistry

Our experiment was compromised somewhat by the complete mortality of fish from one treatment. Nevertheless, we were still able to identify significant differences in the elemental composition of otoliths from fish reared under the three remaining regimes of temperature and salinity. The effects were recognizable even though the same water source was used for all treatments, with the different conditions being determined only by dilution with deionized water and (or) heating.

Comparison of the elemental composition of otoliths from treatments 1 (20°C, 26‰) and 2 (20°C, 35‰), allowed us to assess the influence of salinity. The univariate analyses of single isotopes suggested that salinity caused only subtle differences amongst different isotopes, most evident for ^{31}P, ^{55}Mn, and ^{65}Cu. Nevertheless, when the numerous differences amongst different isotopes were combined into multivariate descriptions, the extent of the difference between treatments became apparent. There was no evidence from any of our analyses that the fish or otoliths differed in growth rates between these salinity treatments. Therefore, the most likely explanation for the elemental

Fig. 2. Plot of the first two canonical variates from a CDA comparing the elemental composition of otoliths amongst the three experimental treatments. Open circles relate to treatment 1, 20°C and 26‰ salinity; solid squares to treatment 2, 20°C and 35‰ salinity; and solid circles to treatment 3, 25°C and 26‰ salinity.

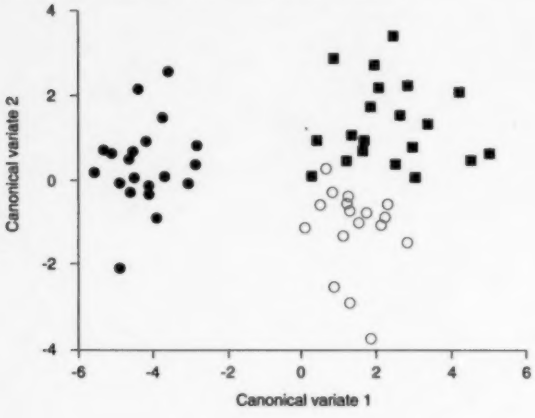
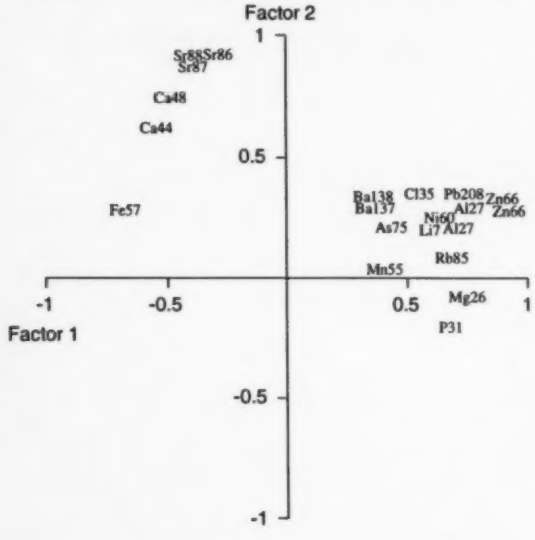


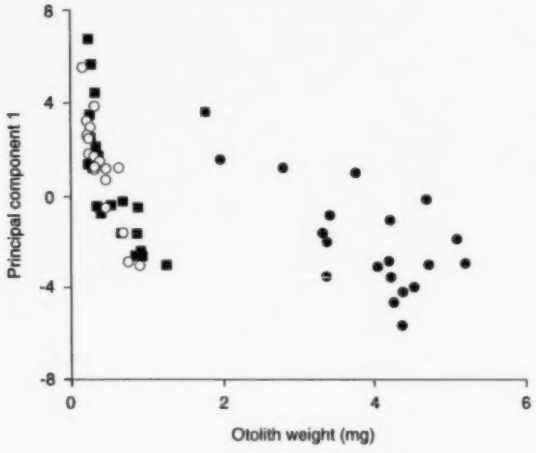
Fig. 3. Plot of first and second factors from the factor analysis indicating affinities amongst the 21 different isotopes measured in juvenile Atlantic croaker otoliths.



differences relates to the different ionic concentrations in the tank water determined by the level of dilution with deionized water. ^{31}P, ^{44}Ca, ^{48}Ca, ^{55}Mn, and ^{65}Cu and the three Sr isotopes all gave higher values in higher salinity. In contrast, ^{26}Mg and ^{85}Rb were recorded at higher levels in the low-salinity otoliths, indicating the influence of some other mechanism, perhaps physiological regulation.

Previous studies have related Sr levels (Coutant and Chen 1993) and Sr/Ca ratios (Radtke et al. 1988; Kalish 1990; Secor 1992) to salinity levels, in each case recording

Fig. 4. Relationship between the first principal component and otolith weight for the three treatments. Open circles relate to treatment 1, 20°C and 26‰ salinity; solid squares to treatment 2, 20°C and 35‰ salinity; and solid circles to treatment 3, 25°C and 26‰ salinity.



higher values from fish collected from higher salinity regimes. Such results have been used to discriminate between anadromous and nonanadromous fish (Kalish 1990) and to identify the timing of migrations between water masses with different salinity regimes (Radtke et al. 1988; Secor 1992; Coutant and Chen 1993). We also recorded higher levels of Sr in the high-salinity treatment but this effect was small compared with that of temperature. Also, since our Sr/Ca ratios were lower from the high salinity treatment, the relative effect of salinity on Ca was higher than on Sr.

The effect of a difference in temperature of 5°C on elemental composition was profound and clearly stronger than that relatable to a 9‰ difference in salinity. The temperature effect was particularly evident for ^{31}P, ^{65}Cu, ^{66}Zn, ^{68}Zn, and the three Sr isotopes. Some of these were at higher concentrations and others at lower concentrations in the higher temperature regime. How temperature might cause such differences is difficult to suggest because of the large number of isotopes involved and their different responses. Furthermore, the effect is confounded with otolith size and growth rate, since fish grew faster and produced larger otoliths at the higher temperature. Numerous authors have previously related Sr/Ca ratios to water temperature suggesting that Sr ions replace Ca ions in the aragonite crystal matrix at a rate controlled by water temperature (Radtke 1984, 1987, 1989; Townsend et al. 1989; Radtke and Shafer 1992). In our study, water temperature clearly affected Sr and Ca levels in the otoliths, but their ratios varied little, suggesting that the deposition rate of both elements responded similarly to the temperature difference, in turn suggesting that in this case Sr/Ca ratios would be poor indicators of water temperature.

The final factor that we identified as influencing the elemental composition of otoliths was otolith size. Within each treatment, and therefore independent of any variation

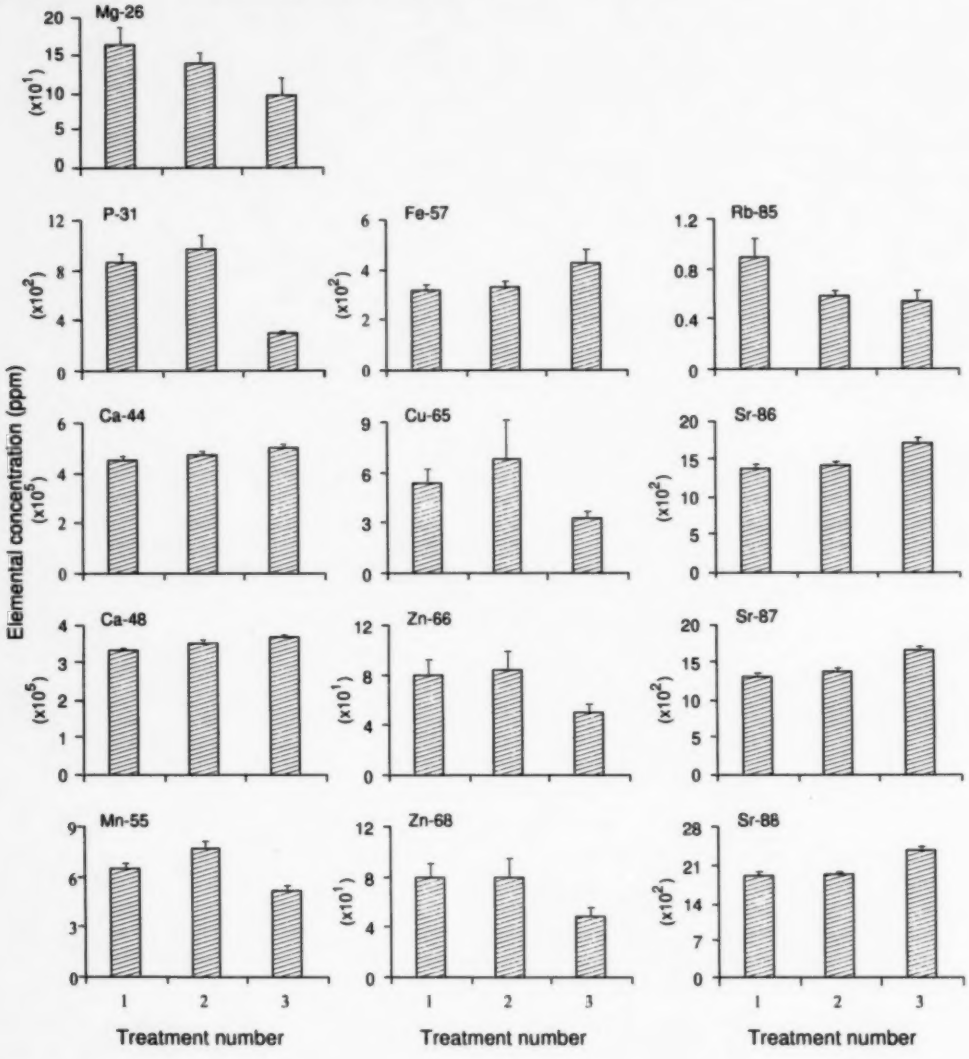
Table 4. ANOVA table examining treatment and tank effects ($\alpha = 0.05$) for each of the 21 isotopes considered in the analysis of otolith microchemistry using solution-based ICPMS.

Isotope	Source	Mean square	F	$p > F$	Pooled
^{7}Li	Treatment	1.1553	2.62	0.2760	
	Tank	0.4403	2.57	0.0855	
	Error	0.1710			
^{26}Mg	Treatment	1.8443	23.28	0.0412	0.0005
	Tank	0.0792	0.37	0.6953	
	Error	0.2143			
^{27}Al	Treatment	1.5493	16.97	0.0557	0.0666
	Tank	0.0913	0.16	0.8517	
	Error	0.5671			
^{31}P	Treatment	8.2579	623.09	0.0016	
	Tank	0.0132	0.11	0.8971	
	Error	0.1219			
^{35}Cl	Treatment	0.1637	3.39	0.2280	0.5015
	Tank	0.0484	0.2	0.8175	
	Error	0.2391			
^{44}Ca	Treatment	0.0494	6.98	0.1253	0.0005
	Tank	0.0071	1.3	0.2817	
	Error	0.0056			
^{48}Ca	Treatment	0.0557	7.53	0.1173	0.0002
	Tank	0.0074	1.37	0.2632	
	Error	0.0054			
^{55}Mn	Treatment	0.6608	12.67	0.0731	0.0001
	Tank	0.0522	0.92	0.4059	
	Error	0.0569			
^{57}Fe	Treatment	0.3533	3.66	0.0323	0.0311
	Tank	0.0724	0.75	0.4771	
	Error	0.0965			
^{60}Ni	Treatment	0.7716	0.79	0.5592	
	Tank	0.9788	2.11	0.1306	
	Error	0.463			
^{65}Cu	Treatment	1.6172	75.5	0.131	0.0399
	Tank	0.0214	0.04	0.9571	
	Error	0.4878			
^{66}Zn	Treatment	1.6506	11.13	0.0825	0.0330
	Tank	0.1484	0.31	0.7325	
	Error	0.4738			
^{68}Zn	Treatment	1.6161	13.17	0.0706	0.0326
	Tank	0.1228	0.27	0.7675	
	Error	0.4617			
^{75}As	Treatment	0.025	0.06	0.9404	0.9170
	Tank	0.3949	1.16	0.3216	
	Error	0.3409			
^{85}Rb	Treatment	1.3156	12.25	0.0755	0.0111
	Tank	0.1074	0.4	0.6731	
	Error	0.2963			
^{86}Sr	Treatment	0.2606	25.55	0.0377	0.0001
	Tank	0.0102	0.51	0.6016	
	Error	0.0199			
^{87}Sr	Treatment	0.2705	15.33	0.0612	0.0001
	Tank	0.0176	0.85	0.4328	
	Error	0.0207			
^{88}Sr	Treatment	0.2461	26.7	0.0361	0.0001
	Tank	0.0092	0.48	0.6234	
	Error	0.0193			
^{137}Ba	Treatment	0.216	0.16	0.8585	0.8011
	Tank	1.3107	1.56	0.2192	
	Error	0.8396			
^{138}Ba	Treatment	0.2557	0.2	0.8354	0.7703
	Tank	1.2975	1.49	0.2334	
	Error	0.8679			
^{208}Pb	Treatment	1.0367	3.3	0.2326	0.3135
	Tank	0.3142	0.35	0.7095	
	Error	0.9097			

Note: The "pooled" column shows the probability for treatment effects when the tank and residual sum of squares were pooled when the probability for a tank effect was >0.2; otherwise it was left blank. Degrees of freedom: treatment, 2; tank, 2; error, 54.

in salinity, temperature, or ionic composition of the water, there was a monotonic relationship between the multielemental composition of the otoliths and their size (and therefore growth rate). This provides strong support for a physiological model that relates otolith chemistry to rates of growth of fish and their otoliths. Previous work based on analyses with the electron microprobe has related Sr/Ca ratios (Gallahar and Kingsford 1992; Sadovy and Severin 1992, 1994), and Na/Ca, K/Ca and S/Ca ratios (Kalish 1989) to fish growth rates. Kalish (1989, 1991*a*) proposed that physiological responses of fish are associated with changes in the chemistry of the blood plasma and endolymph, which are reflected in the rate of ionic deposition in otoliths. This provides a mechanism whereby otolith microchemistry can be correlated with water temperature, because of its influence on fish physiology, but not necessarily directly determined by it (Kalish 1989, 1991*a*; Sadovy and Severin 1992, 1994).

Fig. 5. Comparison amongst the three treatments for the 13 isotopes found to differ significantly by ANOVA. Treatment 1, 20°C and 26‰ salinity; treatment 2, 20°C and 35‰ salinity; treatment 3, 25°C and 26‰ salinity. Note the scales on the abscissae differ.



Ionic contamination of otoliths

To understand the method of contamination of the otolith by many trace elements it is necessary to determine where within the bipartite microstructure the contaminant ions are attached, and how they are chemically bound. From the current understanding of the bipartite microstructure of otoliths (Campana and Neilson 1985; Jones 1986; Morales-Nin 1987) and how these form on a diurnal basis (Mugiya 1985, 1986; Mugiya and Tanaka 1992), three positions where contaminant ions can attach are most likely: within the aragonite crystalline structure, adsorbed to the aragonite microcrystals; and within the proteinaceous matrix. Sr is a likely example of the former (Kinsman and Holland 1969; Radtke and Shafer 1992). Na is more likely to occur within the proteinaceous matrix (Radtke and Shafer 1992). S occurs in the two amino acids, cysteine and methionine, and also in sulphated mucopolysaccharides, which are all components of the organic matrix (Degens et al. 1969; Radtke 1984; Kalish 1989).

That different ions may be located within different parts of the diurnally formed, bipartite structure provides a mechanism for differential deposition rates amongst isotopes. When the relative rates of calcification and matrix production vary, the potential deposition rates of the different ions and the multivariate elemental composition will also vary. Changes to the relative rates of deposition of $CaCO_3$ to protein do occur naturally because of seasonal variation in growth rates (Casselman 1980; Radtke et al.

1985) and as a consequence of laboratory rearing procedures (Kalish 1989). Mugiya and Tanaka (1992) proposed that the formation of the incremental and discontinuous zones of the microincrements in otoliths are likely to be independent and subject to different controlling factors. The rate of production of the organic matrix is a biological process controlled by hormonal and biochemical processes, but the physicochemical process of seeding and growth of aragonitic microcrystals, is likely to be influenced by other processes as well as biological events (Mugiya and Tanaka 1992).

The otoliths of Atlantic croaker that we studied contained many elements and isotopes, mostly at trace levels. In this regard they appear similar to otoliths from other fish species from around the world that have been analysed by microelemental techniques (Papadopoulou et al. 1980; Edmonds et al. 1989, 1991, 1992; Campana and Gagne 1994). If concentrations of some isotopes are compared amongst these studies, differences of as much as several orders of magnitude are apparent. Whilst undoubtedly some of this variation is attributable to different analytical procedures, it is reasonable to conclude that many of the differences are real, reflecting the influence of many factors (Kalish 1991*a*; Radtke and Shafer 1992). Such factors are likely to involve biological ones, such as phylogeny, ontogeny, physiology, age, and diets, as well as physical factors, such as water temperature (Radtke 1984; Radtke and Shafer 1992), salinity (Kalish 1990; Secor 1992), and water chemistry (Kalish 1993). Indeed, the results from our analysis by solution-based ICPMS of otoliths from reared Atlantic croaker have confirmed the influence of temperature, salinity, and growth rates on otolith microchemistry. We also had an opportunity to explore the effects of one more factor on the elemental composition of otoliths: ontogeny. This was done using LA-ICPMS and the results are reported in Fowler et al. (1995).

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References

Beamish, R. 1992. The importance of accurate ages in fisheries science, p. 8-22. *In* D.A. Hancock [ed]. Proceedings of the Australian Society for Fish Biology Workshop on the Measurement of Age and Growth in Fish and Shellfish. Bureau of Rural Resources, Australian Government Publishing Service, Canberra, Australia. Proc. 12.

Bennett, J.T., G.W. Boehlert, and K.K. Turekian. 1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) from $^{210}Pb/^{226}Ra$ measurements in otoliths. Mar. Biol. (Berlin), 71: 209–215.

Campana, S.E., and J.A. Gagne. 1994. Cod stock discrimination using ICPMS elemental assays of otoliths. *In* D.H. Secor, J.M. Dean and S.E. Campana [ed]. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Campana, S.E., and J.D. Neilson. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014–1032.

Campana, S.E., K.C.T. Zwanenburg, and J.N. Smith. 1990. $^{210}Pb/^{226}Ra$ determination of longevity in redfish. Can. J. Fish. Aquat. Sci. 47: 163–165.

Campana, S.E., A.J. Fowler, and C.M. Jones. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. 51: 1942–1950.

Casselman, J.M. 1980. Chemical analyses of the optically different zones in eel otoliths. Ont. Fish. Tech. Rep. Ser. 4: 74–82.

Coutant, C.C., and C.H. Chen. 1993. Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. Can. J. Fish. Aquat. Sci. 50: 1318–1323.

Date, A.R. 1991. Inductively coupled plasma-mass spectrometry. Spectrochim. Acta, Rev. 14(1/2): 3–32.

Degens, E.T., W.G. Deuser, and R. Haedrich. 1969. Molecular structure and composition of fish otoliths. Mar. Biol. (Berlin), 2: 105–113.

Edmonds, J.S., M.J. Moran, N. Caputi, and M. Morita. 1989. Trace element analysis of fish sagittae as an aid to stock identification: pink snapper (*Chrysophrys auratus*) in Western Australian waters. Can. J. Fish. Aquat. Sci. 46: 50–54.

Edmonds, J.S., N. Caputi, and M. Morita. 1991. Stock discrimination by trace-element analysis of otoliths of orange roughy (*Hoplostethus atlanticus*), a deep-water marine teleost. Aust. J. Mar. Freshwater Res. 42: 383–389.

Edmonds, J.S., R.C.J. Lenanton, N. Caputi, and M. Morita. 1992. Trace elements in the otoliths of yellow-eye mullett (*Aldrichetta forsteri*) as an aid to stock identification. Fish. Res. (Amsterdam), 13: 39–51.

Fowler, A.J., S.E. Campana, C.M. Jones, S.R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. 52: 1431–1441.

Gallahar, N.K., and M.J. Kingsford. 1992. Patterns of increment width and strontium:calcium ratios in otoliths of juvenile rock blackfish, *Girella elevata* (M.). J. Fish. Biol. 41: 749–763.

Gunn, J.S., I.R. Harrowfield, C.H. Proctor, and R.E. Thresher. 1992. Electron microprobe microanalysis of fish otoliths—evaluation of techniques for studying age and stock discrimination. J. Exp. Mar. Biol. Ecol. 158: 1–36.

Jarvis, I., and K.E. Jarvis. 1992. Plasma spectrometry in the earth sciences: techniques, applications and future trends. Chem. Geol. 95: 1–33.

Jones, C.M. 1986. Determining age of larval fish with the otolith increment technique. Fish. Bull. U.S. 84: 91–103.

Jones, C.M. 1992. Development and application of the otolith increment technique, p. 1–11. *In* D.K. Stevenson and S.E. Campana [ed.] Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. 117.

Kalish, J.M. 1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132: 151–178.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. U.S. 88: 657–666.

Kalish, J.M. 1991*a*. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph, and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74: 137–159.

Kalish, J.M. 1991*b*. Oxygen and carbon stable isotopes in the otoliths of wild and laboratory-reared Australian salmon (*Arripis trutta*). Mar. Biol. 110: 37–47.

Kalish, J.M. 1993. Pre- and post-bomb radiocarbon in fish otoliths. Earth Planet. Sci. Lett. 114: 549–554.

Kinsman, D.J.J., and H.D. Holland. 1969. The co-precipitation of cations with $CaCO_3$. IV. The co-precipitation of Sr with aragonite between 16° and 96°C. Geochim. Cosmochim. Acta, 33: 1–17.

Morales-Nin, B. 1987. Ultrastructure of the organic and inorganic constituents of the otoliths of the sea bass, p. 331–343. *In* R.C. Summerfelt and G.E. Hall [ed.] The age and growth of fish. The Iowa State University Press. Ames, Iowa.

Mugiya, Y. 1985. Phase difference between calcification and organic matrix formation in the diurnal growth of otoliths in the rainbow trout, *Salmo gairdnerii*. Fish. Bull. U.S. 85: 395–400.

Mugiya, Y. 1986. Effects of calmodulin inhibitors and other metabolic modulators on in vitro otolith formation in the rainbow trout, *Salmo gairdnerii*. Comp. Biochem. Physiol. 84A: 57–60.

Mugiya, Y., and S. Tanaka. 1992. Otolith development, increment formation, and an uncoupling of otolith to somatic growth rates in larval and juvenile goldfish. Nippon Suisan Gakkaishi, 58: 845–851.

Papadopoulou, C., G.D. Kanias, and E. Kassimati. 1980. Trace element content in fish otoliths in relation to age and size. Mar. Pollut. Bull. 11: 68–72.

Pentilla, J., and L.M. Dery. [Ed]. 1988. Age determination methods for Northwest Atlantic species. NOAA Tech. Rep. NMFS72: 135 p.

Quinn, G.P. and R.W. Day. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433–463.

Radtke, R.L. 1984. Cod fish otoliths: information storage structures. Flodevigen Rapportser. 1: 273–298.

Radtke, R.L. 1987. Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6: 19–25.

Radtke, R.L. 1989. Strontium–calcium concentration ratios in fish otoliths as environmental indicators. Comp. Biochem. Physiol. 92A: 189–193.

Radtke, R.L., and D.J. Shafer. 1992. Environmental sensitivity of fish otolith microchemistry. Aust. J. Mar. Freshwater Res. 43: 935–951.

Radtke, R.L., M.L. Fine, and J. Bell. 1985. Somatic and otolith growth in the oyster toadfish (*Opsanus tau* L.). J. Exp. Mar. Biol. Ecol. 90: 259–275.

Radtke, R.L., R.A. Kinzie, III, and S.C. Folsom. 1988. Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fishes, 23: 205–213.

Sadovy, Y., and K.P. Severin. 1992. Trace elements in biogenic aragonite: correlation of body growth rate and strontium levels in the otoliths of the white grunt, *Haemulon plumieri* (Pisces: Haemulidae). Bull. Mar. Sci. 50: 237–257.

Sadovy, Y., and K.P. Severin. 1994. Elemental patterns in red hind (*Epinephalus guttatus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. Can. J. Fish. Aquat. Sci. 51: 133–141.

Secor, D.H. 1992. Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay striped bass *Morone saxatilis*. Fish. Bull. U.S. 90: 798–806.

Secor, D.H., J.M. Dean, and S.E. Campana [Ed]. 1994. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C. 735 p.

Townsend, D.W., R.L. Radtke, M.A. Morrison, and S.C. Folsom. 1989. Recruitment implications of larval herring overwintering distributions in the Gulf of Maine, inferred using a new otolith technique. Mar. Ecol. Prog. Ser. 55: 1–13.

Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS

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Abstract: Laser ablation – inductively coupled plasma mass spectrometry (LA-ICPMS) is a new technique that can be used for the multielemental analysis of otoliths at specific loci. This method was used to sample the otoliths of Atlantic croaker (*Micropogonias undulatus*), reared under different constant regimes of temperature and salinity, to determine whether the elemental composition of otoliths changes ontogenetically. Each otolith was sampled at a number of loci, beginning at the center and then every 500 μm along the longest axis to near the edge; of 23 isotopes measured simultaneously at each locus, 18 were standardized to ^{48}Ca and included in analyses. The elemental composition at otolith centers and near their edges differed significantly amongst treatments, with the effect of temperature a stronger influence. Elemental composition also varied across otoliths from within treatments, indicating endogenous effects. Ontogenetic patterns differed amongst treatments, indicating that endogenous control was mediated by the external environment. Otoliths of fish from one tank where the physical conditions were switched, showed greater variation in the multielemental signal than that resulting only from ontogenetic change. All analyses indicated that otolith formation is the product of numerous interactive exogenous and endogenous processes, including water temperature, salinity, and ontogeny.

Résumé : La spectrométrie de masse avec plasma inductif et ablation au laser est une nouvelle technique qui peut servir à l'analyse multi-élémentaire des otolithes sur des sites précis. Nous avons employé cette méthode pour échantillonner les otolithes de tambours brésiliens (*Micropogonias undulatus*), élevés selon divers régimes constants de température et de salinité, afin de déterminer si la composition élémentaire des otolithes changeait pendant l'ontogenèse. Chaque otolithe a été échantillonné à un certain nombre de sites, tous les 500 μm le long du grand axe, depuis le centre jusque près du bord; sur les 23 isotopes mesurés simultanément à chaque site, nous en avons étalonné 18 par rapport au ^{48}Ca et inclus ceux-ci dans les analyses. La composition élémentaire des otolithes au centre et près des bord différait de façon significative entre les divers régimes, l'influence la plus forte étant celle de la température. La composition élémentaire variait entre les otolithes soumis à un même traitement, ce qui indique l'existence d'effets endogènes. Les profils ontogénétiques différaient entre les traitements, ce qui indique que les effets endogènes étaient régulés par le milieu extérieur. Chez les poissons d'un aquarium dont les conditions physiques avaient été changées, les otolithes présentaient une variation plus grande du signal multi-élémentaire que ce qu'on pouvait attendre du simple changement ontogénétique. Toutes les analyses ont indiqué que la formation des otolithes est le produit d'un grand nombre de processus exogènes et endogènes, notamment la température de l'eau, la salinité et l'ontogenèse.

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Introduction

Current techniques for analysis of the microchemistry of otoliths can be categorized into those for use on whole otoliths and those that sample at specific loci. The former provide a chemical record integrated over a fish's life, whilst the latter provide elemental information for minute parts of an otolith, to address hypotheses relating to age, growth rate, ontogeny, and environmental variation (Radtke 1984, 1989; Kalish 1989, 1991; Gallahar and Kingsford 1992). Unfortunately, the most popular and accessible technique for point sampling otoliths, i.e., X-ray analysis using an electron microprobe, can provide information on only the most abundant elements. It does not have the sensitivity to sample the many trace elements now known to occur in otoliths (Gallahar and Kingsford 1992; Gunn et al. 1992; Campana and Gagne 1994).

A new technique for point sampling solid materials, which may circumvent the limited sensitivity of X-ray analysis is laser ablation – inductively coupled plasma mass spectrometry (LA-ICPMS) (Gray 1985; Denoyer et al. 1991). Here, a high-powered, pulsed laser beam is focused onto a selected position of an otolith. With activation of the laser, causing conversion of photon energy to thermal (kinetic) energy, some of the otolith is vapourized and swept by a flow of argon gas into the plasma where it is atomized and ionized, from which the analyte ions are extracted and analysed by a mass spectrometer (Denoyer et al. 1991; Hall 1992). The otolith surface and the process of ablation can be viewed safely by a remote video camera, whilst electronic stepper motors associated with the stage can be used to focus on different loci.

This technique combines the benefits of point sampling with the sensivity of ICPMS, and avoids the sample preparation by acid dissolution used for solution-based ICPMS (Hall 1992). The technique has proven particularly useful in carbonate analysis, giving accurate estimates of elemental concentrations over several orders of magnitude (Perkins et al. 1991; Pearce et al. 1992). Such success with inorganic carbonates suggested that the technique may also be useful for analysis of biogenic carbonates. Indeed, LA-ICPMS analysis of the nuclei of otoliths from Atlantic cod (*Gadus morhua*), provided "elemental fingerprints" that successfully discriminated amongst different stocks (Campana et al. 1994). Laser ablation has also been used in association with mass spectroscopy to provide estimates of strontium concentration across scales of striped bass (*Morone saxatilis*), successfully discriminating between estuarine and marine fish (Coutant and Chen 1993).

The present study expands upon our earlier analysis wherein we determined that the multielemental composition of whole otoliths was affected by water temperature, salinity, and the growth rate of the fish (Fowler et al. 1995). Here, we assess whether otoliths from the same fish also reflect ontogenetic variation, and determine whether there is an interaction between ontogeny and environmental regimes, by sampling otoliths at particular loci using LA-ICPMS. The specific aims of our analyses here were to determine (1) if the elemental composition at age-specific locations on otoliths varies amongst fish reared in different regimes of temperature and salinity; (2) if the elemental composition varies at different positions on the same otoliths, and whether such ontogenetic patterns differ amongst treatments; (3) whether a switch in environmental conditions causes an identifiable change to otolith elemental composition.

Materials and methods

Juvenile Atlantic croaker (*Micropogonias undulatus*) were reared from hatching for several months under different levels of constant conditions of temperature and salinity. Full details of the spawning and rearing circumstances were presented by Fowler et al. (1995). The conditions of temperature and salinity of the treatments assigned randomly to two tanks each were as follows: treatment 1, 20°C and 26‰; treatment 2, 20°C and 35‰; treatment 3, 25°C and 26‰; treatment 4, 25°C and 35‰. These treatments were maintained for 71 d from 28 October 1992 (day 1) until 6 January 1993 (day 71) under their assigned conditions.

This work also involved one other experimental treatment not previously described. Here, for one tank the environmental conditions were altered through the rearing period, which was longer than for the other four treatments. The initial conditions for treatment 5 were: 25°C and 35‰ maintained from 28 October until 1 December 1992 (day 35) when they were changed to 20°C and 26‰. These were maintained until the 29 December, (day 63) when they were changed back to the original conditions, and subsequently maintained until 27 January 1993 (92 d), when the fish were killed.

Unfortunately, the total loss of fish from both tanks of treatment 4 eliminated the high-temperature, high-salinity treatment. Furthermore, the total loss of fish from one tank of treatment 2 (20°C and 35‰ salinity) reduced the level of replication of this treatment. The otoliths from all fish that died prior to the end of their assigned rearing periods were not considered in the elemental analyses.

Otolith preparation

At the end of the rearing period the surviving fish were killed and measured (standard and total length). The otoliths were removed, washed, air-dried, and weighed (Fowler et al. 1995). One sagitta from each fish was glued to a microscope slide, then ground and polished in the sagittal plane so that the exposed surface was as close as possible to the otolith primordium. This was done by hand using two grades of Imperial lapping film (30 and 3 μm, respectively). Polished otoliths were then sonicated in Super Q water for 3 min, air-dried in a positive flow fume hood, and stored in paper envelopes until ready for analysis.

Laser ablation ICPMS

The LA-ICPMS analyses were done in four blocks of time over a 2-d period (subsequently named in analyses as Block). Within each block of time, otoliths were processed one at a time, taking one from each tank sequentially. Each otolith section was placed within the sample cell, and the laser focused onto the central core. At this time, an argon gas blank was read to determine the current background level for each isotope, which was later used in the blank correction process. The sample site was then hit with two

energy pulses from the laser with a 1-s interval, after which the ablated material was processed by the ICPMS. The pulsed Nd:YAG laser (1064 nM) was run in Q-switched mode at 640 v using a nominal beam diameter of 30 μm. The argon flow rate to the ICPMS was 1.5 L·min^{-1}. The ICPMS was run with 20 channels per atomic mass unit, 7-s peak integration, and a dwell time of 320 μs per channel.

The isotopes sampled were ^{10}B, ^{24}Mg, ^{25}Mg, ^{27}Al, ^{46}Ca, ^{48}Ca, ^{57}Fe, ^{58}Ni, ^{59}Co, ^{60}Ni, ^{65}Cu, ^{66}Zn, ^{69}Ga, ^{85}Rb, ^{86}Sr, ^{87}Sr, ^{88}Sr, ^{118}Sn, ^{121}Sb, ^{137}Ba, ^{138}Ba, ^{207}Pb, and ^{208}Pb. These were chosen from a more extensive list on the basis of a small pilot study involving one otolith. From this test, isotopes that gave low natural levels relative to background or that were confounded with interference molecular ions (Date 1991; Hall 1992), were not subsequently sampled. ^{69}Ga and ^{121}Sb were included as indicators of contamination from the sectioning process, as we had previously determined that they occur at comparatively high levels in the lapping film.

Each otolith was first sampled at the central core and then at intervals of 500 μms along the longest axis, towards the edge. Since the otoliths varied considerably in size (Fowler et al. 1995, Table 2), those from the different treatments were sampled at a different number of loci. The small otoliths from treatments 1 and 2 were sampled at only two positions, those from treatment 3 were sampled at three positions, whilst those from treatment 5 were sampled at four. Otoliths were sampled sequentially taking one per tank, so that sequence effects could subsequently be corrected for.

Table 1. Mean count, SE, and mean count of Ar blanks run before each otolith was assayed, of 23 isotopes sampled from the otoliths of juvenile Atlantic croaker using LA-ICPMS.

Isotope	Mean count	SE	Mean blank count
^{10}B	390	17	217
^{24}Mg	38 865	3 760	503
^{25}Mg	5 872	568	154
^{27}Al	38 756	10 587	11 923
^{46}Ca	6 658	293	1 114
^{48}Ca	283 358	14 422	4 533
^{57}Fe	7 273	158	5 101
^{58}Ni	5 565	226	3 850
^{59}Co	1 663	54	1 370
^{60}Ni	2 073	158	1 237
^{65}Cu	324	58	103
^{66}Zn	1 264	351	180
^{69}Ga	202	57	82
^{85}Rb	272	21	31
^{86}Sr	89 758	5 095	807
^{87}Sr	63 838	3 800	23
^{88}Sr	606 245	31 771	65
^{118}Sn	71	9	51
^{121}Sb	87	10	43
^{137}Ba	244	17	18
^{138}Ba	1 481	112	17
^{207}Pb	167	21	47
^{208}Pb	358	47	85

Note: Data are calculated from all sample positions on all otoliths (n = 202). Only one blank record was recorded prior to sampling each otolith (n = 77).

Data analysis

Output from LA-ICPMS were counts per second for the 23 isotopes indicated above. The counts were corrected for the blank values recorded before each otolith was sampled. In some cases this resulted in negative values where blank values were higher than counts from the otolith. As this presented problems when transforming the data in later analyses, a constant corresponding to the largest negative value + 1 was added to all counts of any isotope where a negative value was generated by the blank-correction process. Finally, since preablation could not be used on small otoliths to ensure the absence of surface contamination (Campana et al. 1994), our data were subjected to outlier analysis to identify potentially spurious values caused by contamination (Tukey 1977). Any value greater than 3 interquartile distances from the 25th or 75th percentiles was rejected (19 of a total of 202 records from all records).

The design of the experiment was originally conceived as a 2 × 2 factorial approach, with temperature and salinity as orthogonal factors. However, the loss of one treatment forced an alteration of the design to a mixed model, with treatment as a fixed effect and tanks nested within treatments. Therefore, the generalized linear model for all hypothesis testing was

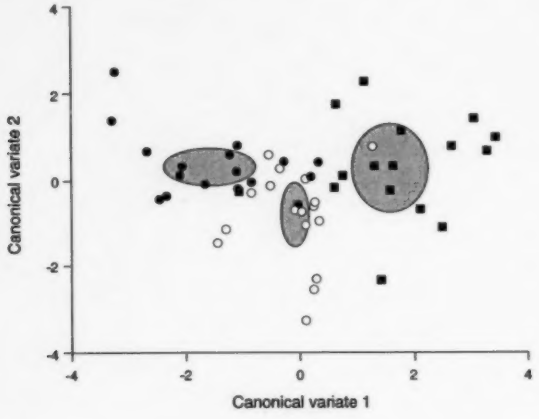
$$[1] \quad Y_{ijklm} = \mu + a_{il} + b_{ij} + c_{ijk} + d_m + \varepsilon_{ijklm}$$

where Y_{ijklm} represents the observation from the lth position on the otolith of the kth fish, from the jth tank nested within the ith treatment; μ is the grand mean; a_{il} measures the fixed effect of position l under the ith treatment; b_{ij} measures the random effect of the jth tank nested within the ith treatment; c_{ijk} measures the random effect of the kth fish within the jth tank under the ith condition; d_m represents the fixed effect of the mth block in which the particular otolith was analysed during the laser ablation process (and assumes no interaction between the block term and any other factor); and ε_{ijklm} represents the random measurement errors, which are assumed to be independent and normally distributed.

Multivariate analysis of variance (MANOVA) was used to test for differences in elemental fingerprints among treatments at particular loci within the otoliths. There were insufficient degrees of freedom to consider tank effects as a nested term in the multivariate model and so individual fish were pooled across tanks with treatment as a fixed factor. The laser sampling was done in four time periods over two consecutive days. Instrument drift across time periods was taken into account by treating these periods as blocks in the MANOVA model (d_m in Eq. 1).

When the MANOVA detected significant treatment effects, canonical discriminant analysis (CDA) was used to display these data in reduced space. The effect of block was removed from the CDA analyses by using the residuals of one-way ANOVAs incorporating the block term as the main factor for each of the isotopes. To determine where

Fig 1. Plot of the first two canonical variates from a CDA comparing the elemental composition at the center of the otoliths. Treatment 1, 20°C and 26‰ salinity (open circles); treatment 2, 20°C and 35‰ salinity (solid squares); treatment 3, 25°C and 26‰ salinity (solid circles).



significant differences among treatments lay, bootstrapped 95% confidence ellipses were calculated on class means on the first and second canonical variates. Canonical scores on both first and second variates were resampled 998 times with replacement, for each of the three treatments (Efron and Gon 1983). When confidence intervals were asymmetric around class means, the largest of the two intervals was used to produce a conservative and symmetric 95% confidence ellipse.

Univariate analyses were performed on each of the isotopes to determine those contributing to the differences detected in the MANOVA. The univariate model was that stated in Eq. 1 with the *l*th term dropped from the model as individual positions on the otoliths were analysed separately. The tank mean square was used as the error term in the test for significance of treatment and type III sums of squares were used throughout because of unequal sample sizes. To allow a more powerful test of treatment effects, tank and residual errors were pooled when the tank effect was not significant with $p > 0.2$. Where significant differences among treatments were detected, means were compared using Tukey's honestly significant difference, applying Kramer's correction for unequal sample sizes (Quinn and Day 1989).

To test for a treatment effect on ontogenetic variation of elemental composition we calculated differences between centers and edges and compared amongst treatments. It was important to use differences in the statistical analyses since assays of multiple ions within a given otolith would be expected to be correlated. Differences were calculated as

$$[2] \quad z_{ijkm} = yc_{ijkm} - ye_{ijkm}$$

where z_{ijkm} represents the difference between the center and edge positions on the otolith of the *k*th fish from the *j*th tank nested within the *i*th treatment and sampled with the laser unit during the *m*th time block, yc_{ijkm} represents the observation from the center position (*c*) and ye_{ijkm} represents the observation from the edge position (*e*). Substituting from Eq. 1 for *y*:

$$[3] \quad z_{ijkm} = (\mu + a_{ic} + b_{ij} + c_{ijk} + d_m + \varepsilon_{ijkmc}) - (\mu + a_{ie} + b_{ij} + c_{ijk} + d_m + \varepsilon_{ijkme})$$

$$[4] \quad = a_{ic} - a_{ie} + \varepsilon_{ijkmc} - \varepsilon_{ijkme}$$

$$[5] \quad = \delta_i + \varepsilon_{ijkm}'$$

Therefore, tank, fish and block effects dropped from the model, and the differences (δ_i) among treatments were compared using a one-way ANOVA.

A similar approach was used when comparing the effects of the switched treatment on otolith microchemistry. Differences were again calculated between adjacent positions on the otolith. On this occasion, however, samples were taken at the center and then every 500 μm out to the edge. As outlined above (Eq. 3), the difference (z_1) between the center (p) and the adjacent position 500 μm from the center (q) is

$$[6] \quad z_{1ijkm} = a_{ip} - a_{iq} + \varepsilon_{ijkmp} - \varepsilon_{ijkmq}$$

$$[7] \quad = \delta_{1i} + \varepsilon_{ijkm}'$$

Similarly, the difference (z_2) between the 500 μm position (q) and the next position (r) is

$$[8] \quad z_{2ijkm} = a_{iq} - a_{ir} + \varepsilon_{ijkmq} - \varepsilon_{ijkmr} = \delta_{2i} + \varepsilon_{ijkm}''$$

In this case ε_{ijkm}' and ε_{ijkm}'' from the same fish are correlated, while errors from different fish are not. Therefore, a MANOVA approach to repeated measures was used to determine if the switched treatment had an effect on otolith composition. Differences (δ_{1i} and δ_{2i}) were treated as dependent variables in the MANOVA with treatment as the main factor.

Multivariate statistical analyses share common assumptions of normality of errors (or multivariate normality) and homogeneity of variance (or equal variance–covariance matrices). Consequently, all elemental ratios to ^{48}Ca were transformed ($y = \log_e x$), after which they were tested by residual analysis and found to conform to the assumptions of the univariate ANOVA. We assumed that this would also ensure the validity of the multivariate tests.

Results

Output from ICPMS after laser ablation at each sample point on each otolith were counts per second for each of the 23 isotopes representing 16 elements. These ranged from <100 to >500 000 counts·s^{-1} encompassing five orders of magnitude (Table 1). ^{69}Ga, ^{118}Sn, and ^{121}Sb consistently gave the lowest values; ^{10}B, ^{46}Ca, ^{57}Fe, ^{58}Ni, ^{65}Cu, ^{85}Rb, ^{137}Ba, ^{138}Ba, ^{207}Pb, and ^{208}Pb had counts in the range of 10^2–10^3·s^{-1}; ^{24}Mg, ^{25}Mg, ^{27}Al, ^{86}Sr, and ^{87}Sr had counts in the range of 10^4–10^5·s^{-1}; only ^{48}Ca and ^{88}Sr were present at levels of >10^5 counts·s^{-1}. The three isotopes ^{27}Al, ^{69}Ga, and ^{121}Sb were excluded from subsequent analyses as they occurred in high concentrations in either the lapping film, glue or glass slides. ^{118}Sn was excluded as it did not exceed background levels.

Table 2. ANOVA table examining treatment and tank effects ($\alpha = 0.05$) for each of the 18 isotopes considered in the analysis of otolith chemistry, at both the center and edge positions, using LA-ICPMS.

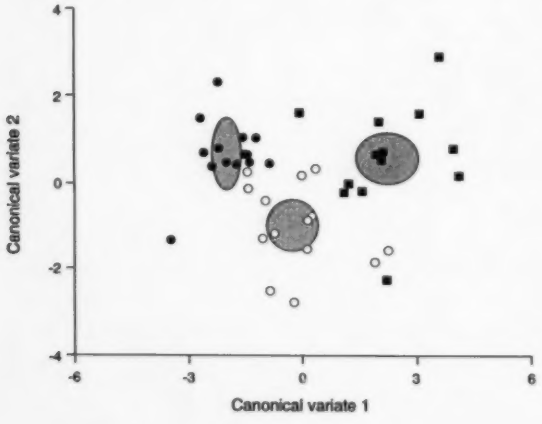
		Center				Edge			
Isotope	Source	MS	*F*	*p* > *F*	Pooled	MS	*F*	*p* > *F*	Pooled
^{10}B	Treatment	0.2608	1.27	0.4409	0.5807	1.0636	24.06	0.0399	
	Tank	0.2057	0.48	0.6223		0.0442	0.14	0.8693	
	Error	0.4293				0.3145			
^{24}Mg	Treatment	1.7115	19.68	0.0484		2.0902	5.58	0.1519	0.0225
	Tank	0.0870	0.14	0.8677		0.3743	0.69	0.5064	
	Error	0.6110				0.5412			
^{25}Mg	Treatment	4.2144	4.25	0.1906	0.0078	5.0457	14.24	0.0656	0.0005
	Tank	0.9926	1.32	0.2766		0.3543	0.65	0.5252	
	Error	0.7517				0.5418			
^{46}Ca	Treatment	0.0098	0.57	0.6356	0.7564	0.0891	2.56	0.2807	0.0363
	Tank	0.0172	0.40	0.6714		0.0132	0.11	0.8971	
	Error	0.0427				0.0278			
^{57}Fe	Treatment	0.5834	1.07	0.4830	0.2047	0.1133	0.34	0.7462	0.7557
	Tank	0.5450	1.33	0.2752		0.3330	0.97	0.3882	
	Error	0.4111				0.3441			
^{58}Ni	Treatment	0.4179	2.14	0.3189	0.7083	0.4337	0.8	0.5568	0.6510
	Tank	0.1957	0.18	0.8323		0.5448	0.58	0.5656	
	Error	1.0621				0.9432			
^{59}Co	Treatment	0.0851	0.18	0.8476	0.8315	0.9059	0.73	0.5777	0.4138
	Tank	0.4735	0.60	0.5545		1.2394	1.46	0.2428	
	Error	0.7939				0.8464			
^{60}Ni	Treatment	0.7899	0.89	0.5299	0.2874	0.7969	0.28	0.782	
	Tank	0.8905	1.09	0.3454		2.8581	5.03	0.11	
	Error	0.8192				0.5682			
^{65}Cu	Treatment	1.3853	0.88	0.533		0.6381	2.47	0.2886	0.1455
	Tank	1.5811	1.69	0.1950		0.2588	0.87	0.4279	
	Error	0.9347				0.2988			
^{66}Zn	Treatment	0.0165	0.07	0.9384	0.9562	2.2528	11.38	0.0808	0.3411
	Tank	0.2509	0.28	0.7566		0.1987	0.31	0.7377	
	Error	0.8943				0.6459			
^{85}Rb	Treatment	0.2897	1.74	0.3656	0.4609	0.2489	26.75	0.036	
	Tank	0.1669	0.44	0.6472		0.0093	0.05	0.9501	
	Error	0.3802				0.1815			
^{86}Sr	Treatment	0.0834	1.24	0.4462		0.0182	4.45	0.1835	0.5782
	Tank	0.0672	1.79	0.1784		0.0041	0.12	0.8836	
	Error	0.0376				0.0330			
^{87}Sr	Treatment	0.1310	0.84	0.5420		0.0950	47.07	0.0208	
	Tank	0.1551	4.73	0.0133		0.0020	0.05	0.9508	
	Error	0.0328				0.0400			

Table 2 (*concluded*).

		Center				Edge			
Isotope	Source	MS	*F*	$p > F$	Pooled	MS	*F*	$p > F$	Pooled
^{88}Sr	Treatment	0.0241	1.62	0.3813	0.4187	0.0425	7.89	0.1114	0.1768
	Tank	0.0149	0.53	0.5938		0.0053	0.22	0.8052	
	Error	0.0282				0.0245			
^{137}Ba	Treatment	0.3772	2.53	0.2836	0.4800	0.0460	0.42	0.7026	0.8832
	Tank	0.1493	0.28	0.7541		0.1086	0.29	0.7528	
	Error	0.5259				0.3798			
^{138}Ba	Treatment	2.1439	11.64	0.0791	0.0113	0.1673	16.13	0.0584	0.5851
	Tank	0.1842	0.42	0.6617		0.0104	0.03	0.9693	
	Error	0.4424				0.3324			
^{207}Pb	Treatment	0.3967	0.84	0.5438	0.5492	0.9834	0.84	0.5440	
	Tank	0.4729	0.56	0.5746		1.1733	2.25	0.1176	
	Error	0.8437				0.5208			
^{208}Pb	Treatment	1.1794	2.09	0.3232	0.1223	1.5865	0.92	0.5198	
	Tank	0.5633	0.84	0.4363		1.7172	2.87	0.0678	
	Error	0.6676				0.5982			

Note: The "pooled" column in each case shows the probability for treatment effects when the tank and residual mean squares were pooled when the probability of a tank effect was >0.2, otherwise left blank. Degrees of freedom: treatment, 2; tank, 2; error, 48 (center) and 42 (edge).

Fig. 2. Plot of the first two canonical variates from a CDA comparing the elemental composition at the position sampled closest to the edge. Treatment 1, 20°C and 26‰ salinity (open circles); treatment 2, 20°C and 35‰ salinity (solid squares); treatment 3, 25°C and 26‰ salinity (solid circles).



Positional variation amongst treatments

Otolith centers

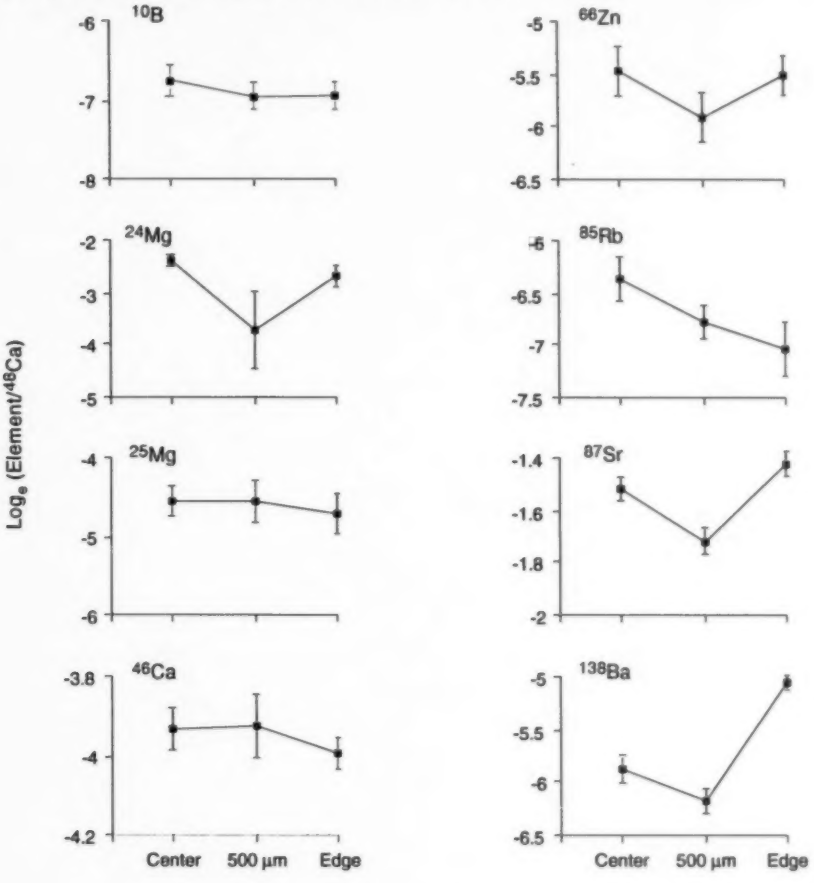
Elemental composition of otolith centers differed significantly amongst treatments (MANOVA, Pillai's trace = 1.0108, $F = 1.76$, df = 36, 62, $p = 0.025$), and the CDA plot indicated considerable separation amongst all the three treatments (Fig. 1). Class means of the three treatments differed significantly as none of the 95% confidence intervals overlapped. These means were spread evenly along the first canonical variate, indicating that there were influences of both temperature and salinity loading on this variate. The confidence ellipses overlapped on the second variate suggesting little separation in this plane.

Univariate ANOVAs detected significant differences among treatments for ^{24}Mg, ^{25}Mg, and ^{138}Ba (Table 2). For each of these the standardized values were higher in the low-temperature treatments than the high-temperature treatment, although Tukey's HSD was not powerful enough to distinguish among treatments. There was little difference between the means for treatments 1 and 2, attributable to the salinity regimes.

Otolith edges

Elemental fingerprints from the otolith edges also differed significantly amongst treatments (MANOVA, Pillai's trace = 1.3913, $F = 3.17$, df = 36, 50, $p < 0.0001$). The CDA plot showed clearer separation amongst all three treatments than was achieved for the center position (Fig. 2). Furthermore, there was less within-treatment variability in elemental fingerprints, reflected in the smaller confidence ellipses. The relationships among treatments were similar to those for the center position. The three treatments showed some separation along the first canonical variate, with treatment 1 falling between treatments 2 and 3, suggesting that the first canonical variate was influenced by both temperature and salinity. Canonical variate 2 also separated treatment 1 from the other two treatments, perhaps reflecting

Fig. 3. Comparison of the means (±SE) of the transformed, standardised data for eight isotopes at the three positions sampled in otoliths from treatment 3.



an interactive influence between temperature and salinity. The univariate analyses indicated significant differences for five isotopes: ^{10}B, ^{24}Mg, ^{25}Mg, ^{46}Ca, and ^{66}Zn (Table 2). The first four of these were more abundant in the otoliths from low-temperature treatments, and no obvious differences amongst means were attributable to salinity.

Ontogenetic variation amongst treatments

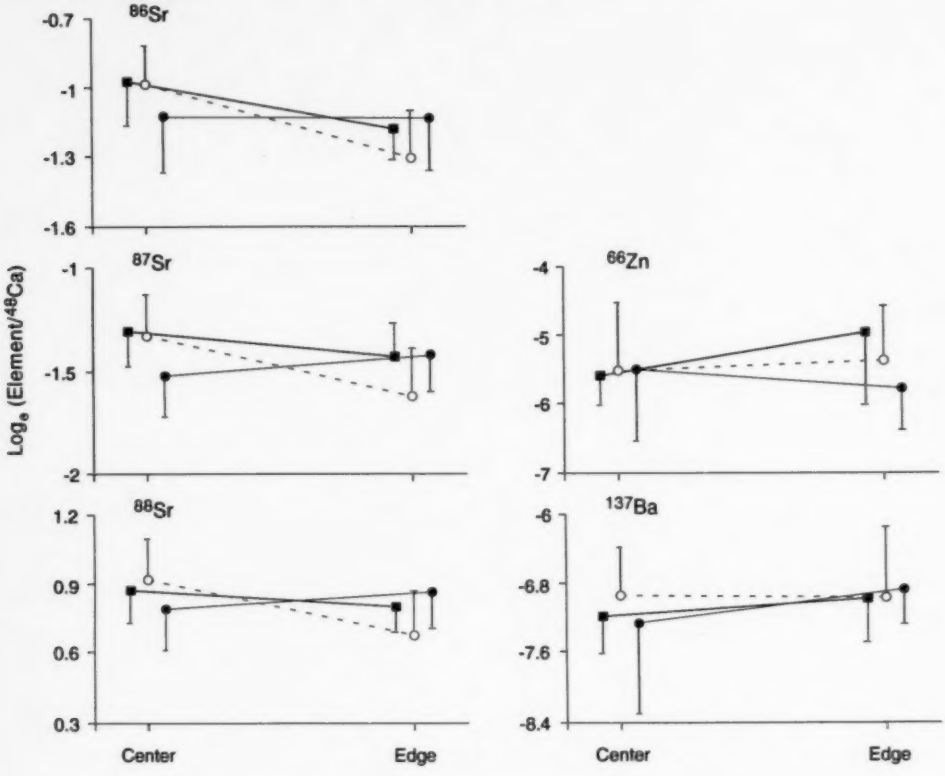
Elemental composition varied amongst sample loci within the same otoliths. For example, the standardized amounts of eight isotopes recorded at the three sample positions for fish from treatment 3 are shown in Fig. 3. Whilst three isotopes show only a minor reduction between the center and edge, four isotopes decreased between the center and 500-µm position and subsequently increased at the edge. ^{85}Rb presented an alternative ontogenetic pattern by decreasing consistently from the center to the edge.

Ontogenetic variation differed amongst treatments. To determine whether this was statistically significant, we compared the differences between the centers and edges for each isotope amongst treatments using one-way ANOVAs. Five isotopes gave significant differences: ^{66}Zn (F = 3.25, df = 2, 41, p = 0.049), ^{86}Sr (F = 6.34, df = 2, 41, p = 0.004), ^{87}Sr (F = 8.87, df = 2, 41, p = 0.0006), ^{88}Sr (F = 6, df= 2, 41, p = 0.0052) and ^{138}Ba (F = 8.7, df = 2, 41, p = 0.0007). Multiple comparisons amongst means generally stressed that treatment 3 was different from treatments 1 and 2, implicating water temperature as the stronger treatment effect on ontogenetic patterns (Fig. 4).

Analysis of switched environmental conditions

For one of the rearing tanks the environmental conditions were switched through its rearing period to determine whether this altered the elemental composition of the otoliths sufficiently to be detectable by LA-ICPMS. On the basis of our earlier results (Figs. 3 and 4), it is likely there would be considerable ontogenetic variation across these large otoliths. Consequently, the effect of the switch in environmental conditions could only be assessed relative to such ontogenetic variation. Here, we used the results from treatment 3 as a control to assess the extent of change across otoliths from treatment 5. Fish from treatment 5 were

Fig. 4. Comparison of the mean (±SE) levels for the five isotopes whose difference between the centers and edges differed significantly amongst treatments. Treatment 1, 20°C and 26‰ salinity (open circles); treatment 2, 20°C and 35‰ salinity (solid squares); treatment 3, 25°C and 26‰ salinity (solid circles).



older and larger than those from treatment 3, although their otoliths had grown at the same average rate (0.035 mm·day^{-1}), suggesting that it would be unlikely that any difference in elemental composition was attributable to a difference in otolith growth rate.

Principal components analysis was used to reduce the dimensionality of the data, and to assess the extent of change in elemental composition across otoliths. The first principal component accounted for 36.2% of the variability, whilst the first and second together accounted for 54.3%. Variation in both principal components across the sample positions for otoliths from both treatments reinforced the significance of ontogenetic variations (Fig. 5). Also, both principal components show clear separation between treatments, particularly at 500 μm from the center, the position where we expected the effect of the switch in environmental conditions to be manifested. Both principal components were compared independently between treatments using a MANOVA. No significant difference was found for the first principal component ($p = 0.7240$), but there was a significant difference for the second principal component ($p = 0.0336$). This is likely to be at least partly a consequence of the switch in treatment, whose effect was concentrated between the center and the 500-μm position.

To isolate which isotopes contributed most to the treatment effects, the difference between the 500-μm position and the center, and between 500 and 1000 μm for each otolith were calculated, and compared independently between the two treatments using a MANOVA. Of the 18 isotopes, only ^{86}Sr ($F = 6.1689$, df = 2, 22, $p = 0.0075$) and ^{87}Sr ($F = 4.7563$, df = 2, 22, $p = 0.0192$) differed between treatments. The differences between the center and 500-μm position were greater from the switched treatment than from treatment 3 (Fig. 6). This suggests that the relative amounts of ^{86}Sr and ^{87}Sr in the otolith matrix changed because of the switch in conditions from 25°C and 35‰ to 20°C and 26‰.

Discussion

The usefulness of studies of microelemental composition of otoliths for retrospective determination of the early life history of wild fish depends on the extent to which the chemical signal can indicate when and how long fish were associated with different water masses. However, numerous factors such as water temperature, salinity, and growth rates complicate this by affecting the rate of deposition of elements in otoliths (Kalish 1991; Radtke and Shafer

1992). We previously quantified variation in trace element inclusion rates due to temperature, salinity, and growth rate by rearing larval Atlantic croaker under constant physical regimes (Fowler et al. 1995). Here, the second otolith from each of the same fish was sampled using LA-ICPMS to point sample age-specific loci, to test hypotheses relating to the ontogenetic variation across otoliths, and the interaction of ontogeny and environmental conditions.

Factors affecting otolith microchemistry

At the center of the otoliths the multielemental signal differed amongst the three treatments. Here the broad beam of the laser (30 μm) clearly sampled otolith material deposited over numerous days, thus swamping the fact that all fish had spent their first 24 h in the same environmental conditions. A multivariate pattern similar to the otolith centers was also obtained for the edges, although these latter results were inherently less variable than the former. In both cases, different temperature and salinity regimes resulted in subtle differences for particular isotopes, which nevertheless combined in the multivariate comparisons to give obvious differences. Canonical discriminant analyses did not indicate a stronger influence of either temperature or salinity, but the differences amongst treatments identified for several isotopes using univariate techniques indicated that the larger effects were attributable to the temperature difference. This reinforces our observation made from analyses of whole otoliths by solution-based ICPMS that the effect of temperature was stronger than that of salinity (Fowler et al. 1995).

The otolith centers (the material from the youngest stage) and the edges (the oldest stage) presented similar multivariate patterns. This indicated that, from the initiation of otolith formation through until near the end of the rearing period, the different environmental conditions influenced the rate of ionic inclusion. Such treatment effects were evident despite intraotolith variation, as elemental composition of otoliths is known not to be homogeneous with respect to age (Kalish 1989).

By point sampling different loci on the same otoliths we identified significant variation in the elemental composition across otoliths. Because environmental conditions were constant through the rearing period this variation must have resulted from intrinsic ontogenetic influences under endogenous control. Previous studies have documented cross-otolith patterns for Sr/Ca ratios (Radtke 1984, 1987, 1989; Radtke et al. 1990; Gallahar and Kingsford 1992). However, all such analyses were done on otoliths from wild fish, making it impossible to distinguish ontogenetic variation from that related to natural environmental influences. Indeed, for most of the above-mentioned studies the Sr/Ca ratios were interpreted to be the direct consequence of variation in water temperature. The possible effect of natural ontogenetic variation was not considered.

Ontogenetic patterns varied amongst different rearing conditions, indicating that the endogenous control referred to above must be mediated by exogenous influences from the environment. This idea of an interactive effect between ontogeny and the environment on elemental composition of otoliths was strongly supported by the results from our "switched" treatment tank, where an alteration in environmental conditions exacerbated the variation in otolith elemental composition beyond the level due to ontogeny alone.

Fig. 5. Comparison of the first and second principal components amongst sample positions from treatment 3 (shaded squares) and treatment 5 (open circles).

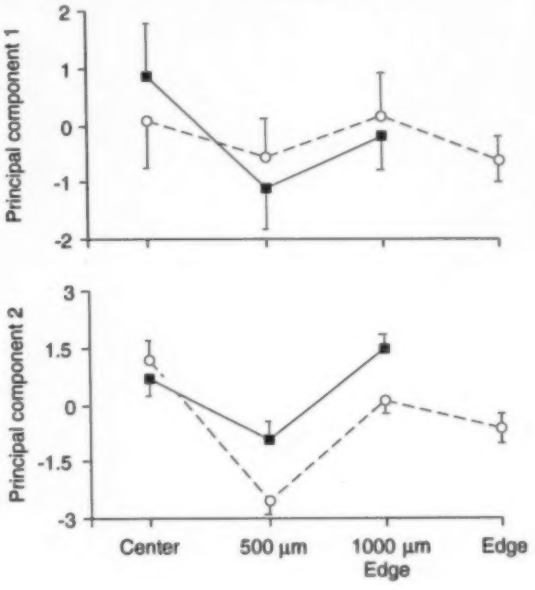
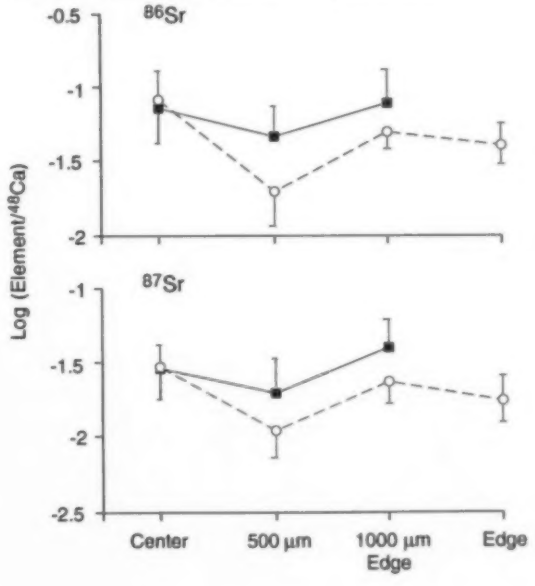


Fig. 6. Comparison of the amounts of ^{86}Sr and ^{87}Sr at the different sample loci across otoliths from treatments 3 (shaded squares) and treatment 5 (open circles).



In our previous paper we suggested that the salinity effect was related to the different ionic concentrations determined by the level of dilution with deionized water (Fowler et al. 1995). We cannot tell whether the relative isotopic concentrations in otoliths are proportional to the isotopic concentrations in the water, or whether those in the otoliths reflect a biological response to these concentrations.

Determining how water temperature influences the elemental composition of otoliths is difficult. Numerous studies have suggested that Sr/Ca ratios are the direct consequence of water temperature, suggesting that the rate at which Sr replaces Ca in the aragonite matrix is temperature dependent (Radtke 1984, 1987, 1989; Radtke et al. 1990; Radtke and Shafer 1992; Townsend et al. 1989). Alternatively, Kalish (1989, 1991) proposed a "physiological" model to account for Sr/Ca ratios that relates physiological changes to changes in the chemistry of blood plasma, which affects the chemical composition of the endolymph and ultimately that of the elemental composition of the otolith. This model has been supported by relationships between Sr/Ca ratios and otolith growth for different species (Sadovy and Severin 1992, 1994; Gallahar and Kingsford 1992).

For us, determining the influence of temperature is even more difficult for several reasons. Firstly, we have identified that many ions contaminate the otoliths of Atlantic croaker, down to trace levels of concentration. However, the mechanisms of inclusion of such ions and where they are located within the otolith microstructure are unknown (Radtke and Shafer 1992; Fowler et al. 1995). Furthermore, the effect of temperature is correlated with and confounded by otolith growth rate. As we suggested previously (Fowler et al. 1995), the elemental differences may be at least in part a consequence of their different sizes and growth rates. We proposed a model that related the amounts of different ions to the relative growth rates of the crystalline incremental and proteinaceous matrix zones of the diurnal bipartite increments of otoliths. Since the otoliths from our high- and low-temperature treatments differed in size, the widths of their daily increments must also have been different. Perhaps, also the relative widths of the different zones comprising the daily increments vary, affecting the potential contamination rates by the ions that contaminate the different zones.

Advantages and constraints of LA-ICPMS

As a new point-sampling method to describe otolith microchemistry LA-ICPMS has some advantages over the electron microprobe (cf. Gunn et al. 1992). Here, preparation of otoliths was simple, involving only hand grinding, polishing, and ultrasonic cleaning. The sampling process itself, which involved placing the otolith into the sample cell, followed by laser ablation and processing was fast and easy. We sampled 77 otoliths at a total of more than 200 sample loci, in four sessions over 2 d, obtaining estimates of 23 isotopes per locus. In comparison, preparation of sections for microprobe analysis is critical and time-consuming as the otolith surface must be as smooth and clean as possible because of the sensitivity of the technique to topographic irregularities (Gunn et al. 1992). Processing time also is likely to be longer because of the requirement for a specimen chamber vacuum. Finally, the electron microprobe has sensitivity to sample only those elements that are major constituents, such as Ca, Sr, and Na that occur in otoliths at concentrations of greater than about 300 ppm. It cannot measure the many elements that occur in otoliths at trace levels or discriminate amongst isotopes of a given element (Edmonds et al. 1991; Campana and Gagne 1994; Campana et al. 1994).

There are, however, disadvantages of LA–ICPMS. Since the laser beam has a diameter of approximately 30 μm, it operates at a relatively large lateral spatial scale, providing an "elemental fingerprint" that integrates over many days. The laser beam was also quite destructive, restricting its use to only two pulses per sample locus, separated by distances of 500 μm across the otolith surface. For many of our small otoliths this still caused substantial damage, sometimes blasting large sections of the otoliths from the surrounding resin. This was not a problem for the larger otoliths. By comparison the spatial resolution and destructiveness of the electron microprobe is far less, allowing elemental analysis to be resolved on a much finer temporal scale (Kalish 1989; Gallahar and Kingsford 1992; Gunn et al. 1992).

This study supported the view that control of otolith microchemistry is complex, and the consequence of numerous interactive factors (Kalish 1991; Radtke and Shafer 1992). Through these analyses we clearly identified the influence of exogenous factors, i.e., water temperature and salinity and the endogenous effect of ontogeny. To these can be added the within-treatment growth rate effect, that we identified from solution-based analyses (Fowler et al. 1995). The complexity is best exemplified by the extent to which ontogenetic patterns were controlled by different physical regimes. These studies have answered numerous questions about otolith microchemistry, but in so doing have also highlighted a number of areas where our knowledge is lacking. These include dissociating the effect of temperature and growth rate and determining where and how contaminant ions attach in the otolith microstructure. Perhaps the refinement of laser techniques, through the reduction of beam width and destructiveness (Hall 1992; Huang et al. 1993), will allow a finer level of resolution of analysis, to help address these questions.

Acknowledgements

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References

Campana, S.E., and J.A. Gagne. 1994. Cod discrimination using ICPMS elemental assays of otoliths. p. 671–691. *In* D.H. Secor, J.M. Dean and S.E. Campana [ed]. Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C.

Campana, S.E., A.J. Fowler, and C.M. Jones. 1994. Otolith elemental fingerprinting for stock identification of Atlantic cod (*Gadus morhua*) using laser ablation ICPMS. Can. J. Fish. Aquat. Sci. 51: 1942–1950.

Coutant, C.C., and C.H. Chen. 1993. Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. Can. J. Fish. Aquat. Sci. 50: 1318–1323.

Date, A.R. 1991. Inductively coupled plasma-mass spectrometry. Spectrochim. Acta Rev. 14(1/2): 3–32.

Denoyer, E.R., K.J. Fredeen, and J.W. Hager. 1991. Laser solid sampling for inductively coupled plasma mass spectrometry. Anal. Chem. 63: 445A–457A.

Edmonds, J.S., N. Caputi, and M. Morita. 1991. Stock discrimination by trace-element analysis of otoliths of orange roughy (*Hoplostethus atlanticus*), a deep-water marine teleost. Aust. J. Mar. Freshwater Res. 42: 383–389.

Efron, G., and G. Gon. 1983. A leisurely look at the bootstrap, the jackknife and cross-validation. Am. Stat. 37: 36–48.

Fowler, A.J., S.E. Campana, C.M. Jones, and S.R. Thorrold. 1995. Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS. Can. J. Fish. Aquat. Sci. 52: 1421–1430.

Gallahar, N.K., and M.J. Kingsford. 1992. Patterns of increment width and strontium : calcium ratios in otoliths of juvenile rock blackfish, *Girella elevata* (M.). J. Fish. Biol. 41: 749–763.

Gray, A.L. 1985. Solid sample introduction by laser ablation for inductively coupled plasma source mass spectrometry. Analyst (Cambridge, U.K.), 110: 551–556.

Gunn, J.S., I.R. Harrowfield, C.H. Proctor, and R.E. Thresher. 1992. Electron microprobe microanalysis of fish otoliths—evaluation of techniques for studying age and stock discrimination. J. Exp. Mar. Biol. Ecol. 158: 1–36.

Hall, G.E.M. 1992. Inductively coupled plasma mass spectrometry in geoanalysis. J. Geochem. Explor. 44: 201–249.

Huang, Y., Y. Shibata, and M. Morita. 1993. Micro laser ablation – inductively coupled plasma mass spectrometry. 1. Instrumentation and performance of micro laser ablation system. Anal. Chem. 65: 2999–3003.

Kalish, J.M. 1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132: 151–178.

Kalish, J.M. 1991. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph, and otoliths of bearded rock cod, *Pseudophycis barbatus*. Mar. Ecol. Prog. Ser. 74: 137–159.

Pearce, N.J.G., W.T. Perkins, and R. Fuge. 1992. Developments in the quantitative and semiquantitative determination of trace elements in carbonates by laser ablation inductively coupled plasma mass spectrometry. J. Anal. At. Spectrom. 7: 595–598.

Perkins, W.T., R. Fuge, and N.J.G. Pearce. 1991. Quantitative analysis of trace elements in carbonates using laser ablation inductively coupled plasma mass spectrometry. J. Anal. At. Spectrom. 6: 445–449.

Quinn, G.P., and R.W. Day. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59: 433–463.

Radtke, R.L. 1984. Cod fish otoliths: information storage structures. Flodevigen Rapportser. 1: 273–298.

Radtke, R.L. 1987. Age and growth information available from the otoliths of the Hawaiian snapper, *Pristipomoides filamentosus*. Coral Reefs 6: 19–25.

Radtke, R.L. 1989. Strontium–calcium concentration ratios in fish otoliths as environmental indicators. Comp. Biochem. Physiol. 92A: 189–193.

Radtke, R.L., and, D.J. Shafer. 1992. Environmental sensitivity of fish otolith microchemistry. Aust. J. Mar. Freshwater Res. 43: 935–951.

Radtke, R.L., D.W. Townsend, S.D. Folsom, and M.A. Morrison. 1990. Strontium:calcium concentration ratios in otoliths of herring larvae as indicators of environmental histories. Environ. Biol. Fishes, 27: 51–61.

Sadovy, Y., and, K.P. Severin. 1992. Trace elements in biogenic aragonite: correlation of body growth rate and strontium levels in the otoliths of the white grunt, *Haemulon plumieri* (Pisces: Haemulidae). Bull. Mar. Sci. 50: 237–257.

Sadovy, Y., and, K.P. Severin. 1994. Elemental patterns in red hind (*Epinephalus guttatus*) otoliths from Bermuda and Puerto Rico reflect growth rate, not temperature. Can. J. Fish. Aquat. Sci. 51: 133–141.

Townsend, D.W., R.L. Radtke, M.A. Morrison, and S.C. Folsom. 1989. Recruitment implications of larval herring overwintering distributions in the Gulf of Maine, inferred using a new otolith technique. Mar. Ecol. Prog. Ser. 55: 1–13.

Tukey, J.W. 1977. Exploratory data analysis. Addison-Wesley, Reading Mass. 499 p.

Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*)

John M. Emlen

Abstract: In the presence of historical data, population viability models of intermediate complexity can be parameterized and utilized to project the consequences of various management actions for endangered species. A general stochastic population dynamics model with density feedback, age structure, and autocorrelated environmental fluctuations was constructed and parameterized for best fit over 36 years of spring chinook salmon (*Oncorhynchus tshawytscha*) redd count data in five Idaho index streams. Simulations indicate that persistence of the Snake River spring chinook salmon population depends primarily on density-independent mortality. Improvement of rearing habitat, predator control, reduced fishing pressure, and improved dam passage all would alleviate density-independent mortality. The current value of the Ricker α should provide for a continuation of the status quo. A recovery of the population to 1957–1961 levels within 100 years would require an approximately 75% increase in survival and (or) fecundity. Manipulations of the Ricker β are likely to have little or no effect on persistence versus extinction, but considerable influence on population size.

Résumé : En présence de données historiques, il est possible de paramétriser des modèles de viabilité d'une population qui sont de complexité intermédiaire et de les utiliser pour prédire les conséquences de diverses mesures de gestion visant des espèces menacées. Nous avons construit un modèle stochastique général de dynamique des populations tenant compte de la rétroaction sur la densité, de la structure par âge et des fluctuations environnementales autocorrélées; nous l'avons paramétrisé pour obtenir l'ajustement optimal, sur 36 ans, de dénombrements des nids de quinnat (*Oncorhynchus tshawytscha*) de printemps effectués dans cinq cours d'eau de l'Idaho servant d'indicateurs. Les simulations indiquent que la persistance de la population de quinnats de printemps dans la rivière Snake dépend avant tout de la mortalité indépendante de la densité. L'amélioration de l'habitat de grossissement, la lutte contre les prédateurs, la réduction de la pression de pêche et l'amélioration des passes migratoires devraient faire baisser la mortalité indépendante de la densité. La valeur présente du paramètre α de Ricker devrait permettre le maintien du statu quo. Pour que la population remonte en 100 ans au niveau de 1957–1961, il faudrait une hausse d'environ 75% de la survie et/ou de la fécondité. Des manipulations du paramètre β de Ricker n'auront vraisemblablement que peu d'effet sur la persistance par opposition à l'extinction, mais elles auront une influence considérable sur la taille de la population.

[Traduit par la Rédaction]

Introduction

Part of the recovery plan for any endangered species should be a risk assessment in which the probabilities of extinction over some finite period are related to various management options. Such a risk assessment consists of two steps: (1) relating management options to their impact on demographic parameters and (2) determining the relationship between the demographic parameter changes and the prognosis for population persistence. The latter step is generally referred to as population viability analysis (PVA) and it involves the application of population models utilizing the best information on the life history of the species in question.

Population viability analysis has at its disposal several classes of population models. At one extreme are the so-called "systems" models that incorporate significant detail into the processes to be modelled. The salmon life cycle model (SLCM; Lee and Hyman 1992), which includes considerable life-history detail and into which still more detailed submodels can be incorporated, is such a model. At the other extreme are the holistic models that, in theory, trade complexity for generality of application. The theoretical models of Goodman (1987), Ewens et al. (1987),

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and Dennis et al. (1991) are of this type. Both extremes have their advantages and drawbacks. With precise and complete knowledge of parameter values, systems models should be the most accurate. Unfortunately, for most species, many parameter values are little more than educated guesses. This opens the possibility of cascading errors in the projection of future population values. The simpler, holistic models are far less parameter intensive, and occasionally, as with the Dennis model, permit parameterization using time sequence data (see below). Essentially, they are bookkeeping models that optimize accuracy with only the most basic information. But these models generally are too simplistic to be reliable as trend predictors except over short time periods. The Dennis model, for example, does not consider density dependence. Thus, its accuracy falters during periods when the modelled populations rise close to carrying capacity (a later, still unpublished model corrects for this factor; B. Dennis, University of Idaho, Moscow, Idaho, personal communication). In addition, the Dennis model relies on a mathematical convergence (toward the predictions of more detailed and, presumably, accurate models) that requires time and so may be misleading over periods as short as 100 years.

A special situation exists when historical data on population size are available. In such cases it may be possible to utilize models that, while simple, incorporate more of the processes affecting population dynamics than do models of the bookkeeping variety. In this paper, I present such an intermediate model and apply it to the Snake River spring chinook salmon.

The purpose of this work is threefold: (1) to show how existing time sequence data can be used to parameterize a model; (2) to show how the parameterized model can be used to assess future extinction probabilities; and (3) to evaluate the effects on extinction probabilities of altering model parameter values manipulable through appropriate management.

The data utilized were redd numbers in several Idaho "index streams" on the middle fork of the Salmon River supplied by the Idaho Department of Fish and Game for 1957–1992 (Table 1).

The model

In keeping with standard practice in fisheries biology, the basic structure of this model incorporates instantaneous density feedback in early life (Ricker 1958) and continuous hatch-to-adult density feedback (Beverton and Holt 1954). The model also incorporates age structure.

Define the following terms:

$n_f(t)$, $n_m(t)$, $n(t)$ are numbers of female, male, and total spawners in year t,

$N(t)$ is the number of redds produced in year t

$p(t)$ is the proportion of eggs spawned in year t that are female

$\tau(t)$ is the average number of fish hatched per redd in year t that live to age 3, were there no density-dependent mortality

$q_{fi}(t)$ is the probability that a female hatched in year t and still alive at age 3, survives to age i and then spawns

$q_{mi}(t)$ is the equivalent for males

$\beta(t)$ is the Ricker β at time t

$\mu(t)$ is a Beverton–Holt parameter for year t

$\delta(t)$ is the ratio of females to the redds they produce in year t before the influence of density feedback

It follows from the above that

$$N(t) = n_f(t)/\delta(t)$$

in the absence of density feedback. Applying Ricker-type feedback, and allowing for depensatory mortality as well (see Emlen 1984, pp. 117–118):

$$[1] \qquad N(t) = n_f(t)\exp\left\{-\beta(t)n(t)\frac{1+a+bn(t)^2}{1+bn(t)^2}\right\}$$

These redds subsequently produce fry that rear in tributaries, where they experience continuing (Beverton–Holt type) density influences, migrate to sea, and then return to spawn at age 3 (males only), 4, or 5. The number of spawners returning in year t is drawn from the pool produced in years $t-3$, $t-4$, and $t-5$.

Five-year-old females spawning in year t arose from $N(t-5)$ redds produced 5 years before and hence number:

$$N(t-5)\tau(t-5)p(t-5)q_{f5}(t-5)$$

in the absence of density-dependent mortality. When Beverton–Holt density dependence is incorporated, this becomes

$$\frac{\tau(t-5)N(t-5)p(t-5)q_{f5}(t-5)}{1+\mu(t-5)N(t-5)}$$

The total number of female spawners in year t, then, including both five and four year olds, is

$$[2a] \qquad n_f(t) = \frac{\tau(t-5)N(t-5)p(t-5)q_{f5}(t-4)}{1+\mu(t-5)N(t-5)} + \frac{\tau(t-4)N(t-4)p(t-4)q_{f4}(t-4)}{1+\mu(t-4)N(t-4)}$$

and for males is

$$[2b] \qquad n_m(t) = \frac{\tau(t-5)N(t-5)(1-p(t-5))q_{m5}(t-5)}{1+\mu(t-5)N(t-5)} + \frac{\tau(t-4)N(t-4)(1-p(t-5))q_{m4}(t-4)}{1+\mu(t-4)N(t-4)} + \frac{\tau(t-3)N(t-3)(1-p(t-3))q_{m3}(t-3)}{1+\mu(t-3)N(t-3)}$$

The values of τ vary year-to-year, and can be approximated, after Peterman (1981), by

$$[3] \qquad \tau = E(\tau)e^{-\sigma w(t)}, \qquad w(t) \sim N(0,1).$$

The value $E(\tau)$ gives the number of fish per redd surviving to age 3 and is, thus, proportional to the standard Ricker α.

The values of the Beverton–Holt coefficient, μ, also vary with time:

$$[4] \qquad \mu = E(\mu)e^{-\sigma' w'(t)}, \qquad w'(t) \sim N(0,1).$$

To avoid further proliferation of parameters, β was assumed constant.

Equations 1–4 define the general model except for three last considerations. Environmental fluctuations are more

Table 1. Redd counts from five Idaho index streams.

Year	Bear Valley	Elk	Marsh	Sulphur	Upper Big
1957	661	398	458	381	225
1958	312	359	262	131	129
1959	381	458	88	41	88
1960	386	346	299	39	155
1961	675	581	526	121	377
1962	484	426	341	78	223
1963	460	654	372	140	148
1964	576	425	709	49	51
1965	301	203	404	32	73
1966	534	525	406	142	123
1967	445	420	650	134	67
1968	576	483	466	142	90
1969	356	349	222	138	65
1970	334	302	456	93	68
1971	108	173	281	58	32
1972	221	212	312	71	60
1973	387	375	518	78	96
1974	130	108	210	30	28
1975	215	169	201	50	77
1976	76	61	48	14	22
1977	129	86	98	5	9
1978	184	208	270	64	95
1979	69	49	47	15	15
1980	15	8	9	2	19
1981	60	23	63	7	22
1982	39	9	40	3	7
1983	56	38	33	8	27
1984	55	27	60	1	42
1985	134	28	108	10	70
1986	74	55	101	65	67
1987	102	149	150	11	36
1988	283	330	217	41	101
1989	15	35	44	2	30
1990	62	42	57	22	20
1991	47	54	40	26	13
1992	41	57	65	5	22

complex than simple white noise. It is, therefore, appropriate to allow for a certain amount of temporal autocorrelation in the process $w(t)$ (see Eq. 3). Too much generality would reintroduce many more parameters, so we compromise by allowing for a single, 1-year lag correlation, writing

$$[5] \qquad w(t) = \lambda w^*(t-1) + \sqrt{1-\lambda^2}\, w^{**}(t)$$

for use in Eq. 3, where λ is the autocorrelation coefficient and $w^*(t)$, $w^{**}(t) \sim N(0,1)$.

Second, fishing pressure on these populations has declined from about 40–60% to less than 15% over the 1957–1992 period (Charles Petroski, Idaho Department of Fish and Game, Boise, Idaho, personal communication). This decline has been modelled in the simplest manner possible, assuming a linear decrease from 50% in 1957 to 15% in 1992. In addition, effects of dam turbines and screens have been studied by Raymond (1988). Using his data, and lumping data into periods (1964–1970, 1971–1975, 1976–1980, 1981–1985) a regression of −ln(survival to the Snake River) on number of turbine units (x_T) and screens (x_S) yields

$$[6] \qquad y = 2.7009 + 0.0419x_T - 0.0278x_S, \qquad R^2 = 0.951.$$

This relation was used to rescale $E(\tau)$ (Eq. 3) on a year-to-year basis. $E(\tau)$, accordingly rescaled for the last year of data (1992), was used in subsequent population projections.

Finally, $p(t)$ was determined using a binomial distribution with a mean of one-half.

Metapopulation considerations

Spring chinook spawn and spend their early life stages (largely) in tributaries. Therefore, fish inhabiting each tributary might be thought of as comprising a single population unit. However, even if no fish returned to a tributary over a 5-year period (meaning all year-classes have died out), recolonization from other tributaries via straying may stave off extinction.

There is a philosophical issue regarding recolonization by strays that has not been dealt with satisfactorily in the PVA literature. If recolonization is by individuals of different genetic constitution from those whose home turf is being invaded, resulting in genetic change of the native stock, is that native stock enhanced or compromised? In particular, if extinction is avoided by virtue of gradual replacement of the native population by genetically different immigrants, should the local stock nevertheless be considered extinct because its genome no longer exists? Furthermore, how different must the native and immigrant stocks be before we reach this conclusion? This matter is probably not of concern where only natural, wild populations exist because current stray rates are likely to be similar to the historic patterns that, in fact, defined the local stocks (unless some significant anthropogenic habitat alteration has taken place), but the presence of hatchery strays is problematic. To avoid such nasty issues, the current work focuses on index streams largely free of hatchery influence (Bear Valley Creek, Elk Creek, Marsh Creek, Sulphur Creek, and Upper Big Creek) in the middle fork of the Salmon River drainage in Idaho.

Given the paucity of data, straying has to be dealt with in a somewhat simplistic fashion. For example, no consideration is given in the present treatment to variations in stray rate among close versus more distant tributaries, and no consideration is given as to whether immigration is more or less likely into areas of low or high resident population density. These simplifications might have significant impacts on the conclusions reached in this report.

Quinn and Fresh (1984) showed that straying from a local spring chinook population increased with age of the fish and decreased with population size. The relations are close to linear. Hence, I modelled the percent outmigration of the population (Θ) using the function

$$[7] \qquad \Theta = \gamma + \kappa y + \rho n,$$

where y is average age in the population, n is population size (number of potential spawners), and γ, κ, and ρ are parameters to be fit with real time sequence data.

Estimation of model parameters

Because the precise trajectory of a population depends on a series of stochastic events (environmental fluctuations, deviations in sex ratio about a mean, variations from mean straying rates) any appropriate model, of necessity, must be stochastic. As such, each run of the model can be thought of as a random selection from a universe of possible population trajectories specific to the values of the parameters used and the initial population conditions. If, out of 100 runs, 80 result in extinction within 100 years, then the probability of persistence over 100 years can be estimated at 20%. This fact must be reflected not only in population projections, but also when using the existing time sequence data to fit the model parameters.

Initial parameter values ($E(\tau)$, β, $E(\mu)$, etc.) were used, along with output from normal random number generators and redd count data, to generate for each of the five index streams, year-by-year: (1) τ and μ values (Eqs. 3 and 4); (2) predicted number of spawners in the absence of straying (Eq. 2), based on redd counts 3, 4, and 5 years in the past; (3) predicted number of spawners after straying (Eq. 7). Numbers of emigrants were determined using a binomial distribution with parameter Θ, with a binomial (mean = 0.5) split among the sexes. Number of immigrants, male and female separately, were randomly (binomially) determined for each population from the total pool of outmigrants; (4) predicted number of redds (Eq. 1); and (5) squared error (squared difference between predicted and observed redd number). The chain of calculations was repeated over all 36 years for which redd count data were available, and the sum of errors squared tallied. Finally, the above excercise was incorporated into a nonlinear least squares routine (Ecker and Kupferschmid 1983) and run repetitively to find those parameter values that best predicted the 36 years of redd data. This entire procedure was then repeated 100 times, with different random number sequences, to produce 100 equally likely parameter configurations, which thus constituted a probability distribution from which expected (mean) parameter values and confidence intervals could be calculated.

The initial parameter values (input to the best fit routine) were obtained as follows.

Observed spawning groups in the index streams are composed of approximately 2% jacks (3 year olds), and 4 and 5 year olds in a ratio of 0.31:0.67 (C. Petroski, personal communication). Values of $q_{.i}$ were set accordingly.

Initial parameter input values for $E(\tau)$ were based on estimated delta and (Ricker) α-values. Petrosky and Schaller (1995) estimated α for these index streams at between about 1.9 and 2.8. Data collected on spring chinook spawners and redds on the middle fork of the Salmon River in 1988 (T. Bjornn, University of Idaho, Moscow, Idaho, personal communication) indicate a redd-to-spawning female ratio of 3.5 to 4 (but see discussion of redd count data, below). Under present densities of about 40–80 redds per stream and a beta value of 0.002 (see below), this translates to a δ-value of 0.20–0.26. The initial value of δ was set at 0.25. Letting n represent stock, n' recruits, we can write, on average, $n' \approx E(\tau)N = E(\tau)n_f/\delta \approx E(\tau)n/2\delta$ in the absence of density feedback. But also in the absence of density feedback, $n' = \alpha n$. Hence $E(\tau) \approx 2\alpha\delta$. Therefore, $E(\tau)$ lies somewhere in the neighborhood of 0.76–1.46.

Petrosky and Schaller (1995) estimated β-values for these streams (over indexed reaches) as 0.0008–0.0026. The input value used in data fitting for this paper was 0.002.

The initial estimate of $E(\mu)$ was obtained by estimating the historic number of redds per stream at 200, two to four times present levels. Then, if Beverton–Holt feedback reduced the population at those levels by, say, 8–10%, $E(\mu) = -\ln(0.92)/200 = 0.0004$.

With respect to σ and σ', suppose initially that environmental fluctuations result in a 95% confidence swing of 20% about the average values of τ and μ. Then the values of σ and σ' must be on the order of 0.17. The value of the environmental autocorrelation must lie between 0 and 1; a pure guess of 0.4 was used.

A regression of the fraction of the population composed of strays at Cowlitz hatchery (Quinn and Fresh 1984) on average age at return and escapement level provided initial estimates of γ, κ, and ρ of -0.6, 1.00, and -0.0002, respectively. Finally, in the absence of any information as to possible bias of density feedback by depensatory mortality, a and b were set initially to zero.

Constraints utilized in the fitting procedure involved holding $E(\tau)$, β, $E(\mu)$, σ, σ', δ, a, and b, as well as outmigration rate over all years non-negative, and $0 < \lambda < 1$.

Redd count data were based on indexed reaches that constituted different proportions of the various index streams. By treating these counts as absolute, the model, in effect, scales the population counts of the different streams in different units. Therefore, because $E(\tau)$, β, and $E(\mu)$ are in per-individual units, this fact alone leads to different values for these parameters among the streams. Predictions as to probability of persistence or (appropriately weighted) projected redd counts should not be affected.

Table 2. Sensitivity to stray rate.

Stray rate relative to estimated true value	Probability of persistence	Number of redds in year 100 for persisting populations
0.001	0.988±0.012	734.7±14.4
0.5	0.988±0.012	713.2±14.1
1.0	0.986±0.014	709.6±13.9
2.0	0.988±0.012	704.7±14.1

Note: Values are means ± SE.

Table 3. Effects of potential measurement error.

Sigma relative to estimated value	Probability of persistence	Number of redds in year 100 for persisting populations
0.001	0.988±0.012	701.5±13.7
0.500	0.988±0.012	703.8±14.0
1.000	0.988±0.012	720.2±14.3

Note: Values are means ± SE.

Table 4. Fitted parameter values.

Parameter	Population				
	Bear Valley	Elk	Marsh	Sulphur	Upper Big
$E(\tau)$ (1957)	1.028±0.022	1.037±0.015	1.003±0.022	0.988±0.023	1.006±0.015
β	0.003±0.000	0.002±0.000	0.003±0.000	0.004±0.001	0.003±0.000
$E(\mu)$	0.001±0.000	0.001±0.000	0.002±0.001	0.002±0.001	0.001±0.000
σ	0.184±0.010	0.168±0.009	0.174±0.011	0.169±0.010	0.181±0.010
λ	0.403±0.028	0.391±0.023	0.360±0.025	0.405±0.028	0.439±0.025
δ	0.106±0.006	0.110±0.007	0.102±0.007	0.133±0.008	0.141±0.007
σ'	0.184±0.009	0.169±0.007	0.196±0.014	0.194±0.014	0.194±0.011
γ	−0.584±0.046	−0.578±0.043	−0.679±0.048	−0.613±0.057	−0.570±0.038
κ	1.017±0.056	0.992±0.053	1.036±0.058	0.964±0.061	1.071±0.054
ρ	0.001±0.000	−0.000±0.000	−0.001±0.000	−0.000±0.001	−0.001±0.000
a	4.336±0.514	4.612±0.396	4.240±0.486	5.912±0.568	4.942±0.426
b	0.000±0.000	0.000±0.000	0.000±0.000	0.000±0.000	0.000±0.000
α	7.307±0.669	6.831±0.465	8.850±1.213	5.612±0.583	5.139±0.823

Note: Values are means ± SE. Average stray rate (1988–1992) $= [-\bar{\gamma} + \bar{\kappa}(\text{age}) - \bar{\rho}\bar{\delta}(\text{no. redds per population in 1988–1992})]/100$
$= [(-0.6048) + (1.0160)(4.65) - (-0.0002)(0.1184)(66.9)]/100$
$= 0.0412$
Bars indicate average over all five populations.

Results

Sensitivity tests

Because the five index streams do not comprise the full metapopulation, projections of population survival and size based on them might be biased by omission of other streams. It seems likely, because the five populations are positively correlated with respect to year-to-year redd counts and because they are currently well below carrying capacity, that their dynamics are, in fact, nearly independent. That is, metapopulation structure seems likely to prove a minimal factor in population projections, at least so long as the population remains well below historic levels. To test this expectation, 100-year simulations were run, 10 replicates (different w^*, w^{**} sequences) for each of the 100 parameter solution sets, for various stray rates (γ-, κ-, and ρ-values of 0.001, 0.50, 1.00, and 2.00 times their estimated true values), and with $E(\tau)$ set at two thirds of its estimated true value to assure a fair number of extinctions for comparison purposes. All projections were initiated with 5 years (1988–1992) of observed redd counts. The results (Table 2) indicate minimal influence of stray rate. Therefore, simulation bias introduced by incomplete metapopulation data also should be minimal.

There is some question as to the accuracy of the redd counts. The impact of counting error on accuracy of population projections can be explored, at least crudely, as follows. Because redd counts are constrained to be positive, it is not unlikely that the measurement error term should be approximately lognormally distributed. Thus, measurement error affects redd count in the same manner as environmental fluctuations and can be incorporated into the σ term. Population projections were run using σ equal to zero (equivalent to a situation in which all "environmental" error is, in fact, measurement error), equal to its estimated true value (no measurement error), and equal to one half of its estimated true value. The results (Table 3) indicate that extreme count errors may lead to low projections of redd numbers (although the differences for different error rates are statistically insignificant) and have no influence on projected probability of population persistence.

Although the mean best fit parameter values were similar to expectation (initial values used), considerable variation occurred among the 100 solution sets in each of the five populations. This raised the possibility of different solution sets corresponding to different local optima on the response surface. To check for this, frequency distributions were examined for all 12 parameters for each of the five populations. There is no evidence of multimodality in any of the populations. The best fit parameter values are given in Table 4.

Average stray rate is predicted to be about 4%. Data on actual stray rates are poor for the middle fork of the Salmon River, but the expected rate for spring chinook spawning at the Cowlitz hatchery, projected for the population density levels and spawning age structure seen in the index streams, is also about 4% (based on the aforementioned regression of percent strays on population size and age at return (Quinn and Fresh 1984).

Projections

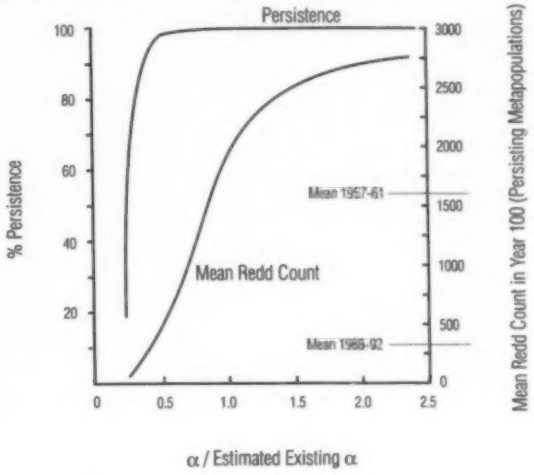
Following the above sensitivity tests and final parameter fitting, simulations were run, again over 100 years and with 10 replicates for each of the 100-parameter solution sets, varying the value of $E(\tau)$ from 0.50 to 2.5 times its estimated value, and letting β range between 0.001 and 5.00 times its estimated value. Results are provided in Figs. 1 and 2.

The parameter $E(\tau)$ is proportional to α and describes density-independent survival and reproductive output. It is convenient, then, to speak of proportional changes in

α rather than $E(\tau)$. Varying $E(\tau)$ (or α, Fig. 1) clearly has a profound influence on both likelihood of persistence and expected redd count in the 100th year. The present estimated α-value apparently is sufficient to virtually ensure population persistence over the next 100 years, and to lead to considerable increases in the number of redds over present counts (1988–1992), the lowest 5-year counts on record. If α were to further decrease to below 0.50 its present level, however, there seems little doubt that extinction would follow. Population recovery, also, might be expected under present α. Indeed, in the absence of adverse weather conditions, environmental deterioration, or unexpected setbacks, the 1957–1961 levels should be regained within about 100 years.

Alterations in β (mediated primarily through increased spawning habitat) seem to have virtually no impact on probability of population persistence. As β varies from 0.001 to 5.00 times its present value, the likelihood of persistence drops from 100 to 95%. On the other hand, a doubling of spawning habitat (halving the present value of β) might increase the redd count by as much as 2.25-fold.

Fig. 1. Relation of persistence probability over 100 years, and expected number of redds in year 100 as a function of α relative to its existing (estimated) value.

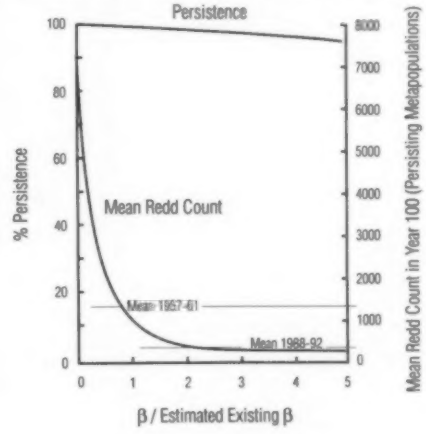


Discussion

On the optimistic side, the model projections indicate a virtually certain persistence of Snake River spring chinook over the next 100 years. Models can be misleading, however. Notice in Fig. 1 that the mean redd count over the last 5 years corresponds to an α-value of only about 0.4 its estimated value. This may be a consequence merely of stochastic events, i.e., the recent redd count does not line up with the estimated α for purely statistical reasons. On the other hand, it could mean that important events, not accounted for in the model, are occurring; that is, parameter values are changing over time. Have we merely witnessed a short series of unusually "unlucky" years, or is something more sinister going on? If the latter is true, then a shift to the right is indicated for the redd count versus α curve, suggesting an even dimmer prognosis for stock recovery. Consider also, when reading predictions from Fig. 1, that as a population grows with increased α, the role of the density feedback parameters, β and $E(\mu)$, becomes increasingly strong. Because of the insensitivity of population dynamics to these parameters at present densities, the values obtained for them using the best fit routines may be inaccurate. Projections of redd counts with high α values, therefore, must be considered tenuous; projections might be either overly pessimistic or overly rosy, and given present data it is impossible to say which.

The analyses and conclusions presented here account for temporal and other stochastic variation over the period between 1957 and 1992. They do not address risk arising from catastrophes. The effects of a series of unusually low water years, high reservoir mortality, a toxicant spill, or any other major environmental disruption might well fall outside the range of fluctuations implied by events over those 36 years and implicitly incorporated into the 100-year projections. Thus the predictions given in Fig. 1 are probably optimistic. In addition, no consideration is given to the importance of maintaining genetic diversity in the populations. While the model predicts little danger

Fig. 2. Relation of persistence probability over 100 years, and expected number of redds in year 100 as a function of β relative to its existing (estimated) value.



of extinction for the population as a whole, local populations can be expected to die out at a more rapid rate and to be recolonized by others. The consequent genetic deterioration can be expected to lower adaptedness and lessen resilience of the species to further environmental change. Again, the projections provided here probably paint an overly optimistic picture of the species' true status. From a management perspective, the projections given in this paper should be considered a best case scenario.

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References

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Lond. Ser. 2: 533.

Chapman, D.W., A. Giorgi, M. Hill, D. Park, W.S. Platts, and K. Pratt. 1990. Prefatory review of status of Snake River chinook salmon. Report prepared by Don Chapman Consultants, Inc., for the Pacific Northwest Utilities Conference Committee, Nov. 13, 1990.

Dennis, B., P.L. Mulholland, and J.M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecol. Monogr. 61: 115–143.

Ecker, J.G., and M. Kupferschmidt. 1983. An ellipsoid algorithm for nonlinear programming. Math. Program. 27: 83–106.

Emlen, J.M. 1984. Population biology: the coevolution of population dynamics and behavior. MacMillan, New York. 527 p.

Ewens, W., P.J. Brockwell, J.M. Gani, and R.I. Resnick. 1987. Minimum viable population size in the presence of catastrophes, p. 59-68. *In* M.E. Soule [ed.] Viable populations for conservation, Cambridge University Press, Cambridge, U.K.

Goodman, D. 1987. Consideration of stochastic demographics in the design and management of biological reserves. Nat. Resour. Modell. 1: 205–234.

Lee, D.C., and J.B. Hyman. 1992. The stochastic life cycle model (SLCM): Simulating the population dynamics of anadromous salmonids. USDA For. Ser. Res. Pap. INT-459.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38: 1113–1119.

Petrosky, C., and H. Schaller. 1995. A comparison of productivities for Snake River and lower Columbia River spring and summer chinook stocks. *In* Proceedings of Salmon Management in the 21st Century. 1992 Northwest Pacific Chinook and Coho Workshop, Boise, Idaho. American Fisheries Society Publication, Idaho Water Resource Research Institute. In press.

Quinn, T.P., and K. Fresh. 1984. Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. Can. J. Fish. Aquat. Sci. 41: 1078–1082.

Raymond, H.L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon in the Columbia River Basin. N. Am. J. Fish. Manage. 8: 1–25.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. J. Fish. Res. Board Can. 119: 1–300.

Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density

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Abstract: Introduced dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) foul native unionid bivalves by attaching to their shells in large clusters and may critically impair many North American unionids that are already threatened by habitat degradation. Using literature and new field data, we examined patterns of *Dreissena* infestation on unionids, and the relationships between *Dreissena* field density, infestation intensity, and unionid mortality. Linear regression models showed that *Dreissena* field density strongly predicts (*i*) the proportion of unionids colonized by dreissenids ($r^2 = 0.90$, $p < 0.0001$) and (*ii*) the mean number of dreissenids attached to unionids ($r^2 = 0.81$, $p < 0.0001$). We fitted a compound Poisson model that accounts for dreissenid clustering and predicts both the proportion of colonized unionids and the mean infestation intensity as effectively as our empirically derived models. The proportion of unionids colonized by *Dreissena* follows a saturation curve, increasing rapidly with *Dreissena* densities up to 200/m^2, and reaching a plateau at 70–80% colonization. Unionid mortality (reflected by the proportion of dead unionids) is strongly correlated with *Dreissena* field density ($r^2 = 0.82$, $p < 0.002$) at densities above 1000/m^2. Our models predict that severe unionid mortality (>90%) occurs when *Dreissena* density and mean infestation intensity reach 6000/m^2 and 100 dreissenids/unionid.

Résumé : Les moules introduites de la famille des Dreissenidés (*Dreissena polymorpha* et *Dreissena bugensis*) nuisent aux bivalves unionidés indigènes, en se fixant en gros paquets sur les coquilles de ces derniers, et peuvent compromettre la survie de nombreux unionidés d'Amérique du Nord qui sont déjà menacés par la dégradation des habitats. À partir des données publiées et de nouvelles données recueillies sur le terrain, nous avons examiné les profils d'infestation des unionidés par les *Dreissena* et les relations entre la densité des *Dreissena* sur le terrain, l'intensité de l'infestation et la mortalité des unionidés. Les modèles de régression linéaire ont montré que la densité sur le terrain des *Dreissena* constitue un fort prédicteur (*i*) de la proportion des unionidés colonisés par les dreissenidés ($r^2 = 0{,}90$, $p < 0{,}0001$ et (*ii*) du nombre moyen de dreissenidés fixés sur les unionidés ($r^2 = 0{,}80$, $p < 0{,}0001$). Nous avons mis au point un modèle composé de Poisson qui rend compte de l'agrégation des dreissenidés et prédit aussi efficacement que nos modèles empiriques la proportion d'unionidés colonisés et l'intensité moyenne d'infestation. La proportion des unionidés colonisés par *Dreissena* suit une courbe de saturation, augmentant rapidement avec la densité des *Dreissena* jusqu'à environ 200/m^2 et atteignant un plateau à 70–80% de colonisation. La mortalité des unionidés (indiquée par la proportion d'unionidés morts) est fortement corrélée avec la densité des *Dreissena* sur le terrain ($r^2 = 0{,}82$, $p < 0{,}002$) aux densités supérieures à 1000/m^2. Nos modèles prédisent qu'une forte mortalité des unionidés (>90%) se produit quand la densité des *Dreissena* et l'intensité moyenne d'infestation atteignent 6000/m^2 et 100 dreissenidés/unionidé.

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Introduction

Freshwater bivalves of the family Unionidae play an important role in nutrient recycling in aquatic systems (Lewandowski and Stanczykowska 1975; Kasprzak 1986; Nalepa et al. 1991*a*) and are potentially valuable indicators of water quality (Imlay 1982; Green et al. 1989). North America has the richest freshwater mussel fauna in the world, with close to 300 described species and subspecies (Williams et al. 1993). However, over the past few decades, unionid abundance and species diversity have severely declined throughout North America, largely because of habitat degradation (Fuller 1974; Nalepa et al. 1991*b*; Williams et al. 1993); 70% of our native unionids are currently considered to be endangered, threatened, or of special concern (Williams et al. 1993).

A new, potentially fatal stress on North American unionid populations has been caused by the introduction of the European zebra mussel, *Dreissena polymorpha* (Hebert et al. 1989). Using their adhesive byssal threads, zebra mussels may attach to any solid substrate, including the shells of other molluscs (e.g., Lewandowski 1976; Mackie 1990). Evidence from field and laboratory studies suggests that zebra mussels preferentially colonize living unionids (Biryukov et al. 1964; Wolff 1969; Lewandowski 1976; Mackie 1990; Ricciardi 1994). Unionids are fouled by byssally attached zebra mussels wherever they are sympatric in Europe (Wagner 1936; Sebestyen 1938; Zhadin and Gerd 1961; Wiktor 1963; Biryukov et al. 1964; Kuchina 1964; Wolff 1969; Lewandowski 1976; Arter 1989) and North America (Hebert et al. 1989, 1991; Mackie 1990; Schloesser and Kovalak 1991; Hunter and Bailey 1992; Tucker 1994; Ricciardi 1994; Gillis and Mackie 1994). The infestation intensity varies by several orders of magnitude among these habitats; in extreme cases, zebra mussels settling on unionid shells may form encrusting colonies of more than 10 000 individuals, and weigh 3–4 times as much as the unionid (Hebert et al. 1991; Schloesser and Kovalak 1991). The more recently introduced quagga mussel (*Dreissena bugensis*) may also contribute to unionid fouling, but probably to a much lesser extent than the zebra mussel because it does not show a preference for unionids as substrates (Conn and Conn 1993). Dreissenid infestations are believed to negatively affect unionids primarily by smothering siphons, preventing valve opening and closure, and interfering with normal feeding and burrowing activity (Mackie 1990; Schloesser and Kovalak 1991; Haag et al. 1993). Heavy infestations of *Dreissena* may cause reduced glycogen reserves (Haag et al. 1993), significant depletion of biomass and total energy stores (A. Ricciardi, in preparation), and shell deformation in unionids (Wolff 1969; Lewandowski 1976; Mackie 1990; Hunter and Bailey 1992). These impacts may have major consequences for unionid populations, as indicated by the significant mortality and loss of species richness that have often followed *Dreissena* invasions (Sebestyen 1938; Arter 1989; Hunter and Bailey 1992; Gillis and Mackie 1994; Haag et al. 1993; Ohnesorg et al. 1993; Maleski and Masteller 1994; A. Ricciardi, in preparation).

Relocation of unionid populations has been advocated as a conservation measure to protect them from *Dreissena* infestation (Waller et al. 1993; Havlik 1994), but since *Dreissena* is expected to successfully invade most North American water bodies (Strayer 1991; Ramcharan et al. 1992), massive relocation of unionids into refugia that are inaccessible to *Dreissena* may be both futile and impractical. Future conservation practices, whatever form they may take, will likely involve decisions regarding levels of *Dreissena* infestation that are tolerable to particular unionid populations. Such decisions will require a method of predicting the level of infestation on unionids prior to a *Dreissena* invasion.

Dreissena population densities are highly variable among different aquatic habitats (Stanczykowska 1977). There has been some recent success in developing predictive models of *Dreissena* abundance from environmental variables (Ramcharan et al. 1992; Mellina and Rasmussen 1994), and more refined models may be available in the future. Therefore, it may be possible to predict the infestation intensity (and correlated impacts) of *Dreissena* on unionids from environmental variables if infestation can be quantitatively related to local *Dreissena* abundance. This would permit us to identify habitats and unionid populations that are at great risk, in advance of a *Dreissena* invasion. The first step in developing these larger predictive models, and the main objective of our investigation, is to quantify relationships between the infestation intensity of *Dreissena* on unionids and *Dreissena* density. Secondly, we examine whether *Dreissena* density and infestation intensity can be used to predict unionid mortality.

Methods

We examined patterns of unionid infestation across a range of habitats and geographic regions, using data obtained from the literature combined with our own field data collected from the St. Lawrence River. The primary data set consisted of 36 records, including 13 from the Laurentian Great Lakes (Hebert et al. 1989, 1991; Schloesser and Kovalak 1991; Gillis and Mackie 1994; Masteller and Schloesser 1992; Haag et al. 1993), 9 from the St. Lawrence River (this study), 8 from the upper Mississippi River Basin (Tucker et al. 1993; Tucker 1994), and 6 from the Mazurian lakes of northeastern Poland (Lewandowski 1976). Data on infestation intensity included (*i*) the percentage of unionids colonized by *Dreissena*, (*ii*) the mean number of dreissenids per unionid (= mean infestation intensity), and (*iii*) the maximum number of dreissenids found on a unionid (= maximum infestation intensity). These data were coupled with estimates of *Dreissena* field density for each site, wherever possible (Table 1); when more than one literature source was required to obtain these data, only data collected within the same year were used. The mean number of dreissenids per unionid includes all unionids (including those not colonized by *Dreissena*) in a given population. The Mississippi River studies (Tucker et al. 1993; Tucker 1994) gave mean infestation intensities for colonized unionids only, and therefore were multiplied by the proportion of colonized unionids to obtain the mean infestation for the entire population.

Data collected from St. Lawrence River sites

Unionids were collected from six sites on the upper St. Lawrence River in Quebec: two sites on Lake St. Louis (near Lachine), one site on Lake St. François (near Les Cèdres), one site at the Port of Montréal, and two sections of the Soulanges Canal at Pointe-des-Cascades (approx. 45°20′N, 73°58′W). Collections at the Soulanges Canal sites were made monthly during the summers (June–August) of 1992–1994. Lake St. François was sampled once in July 1992. Two sites in Lake St. Louis were sampled in September 1992; one of these sites was revisited in June 1994. The Port of Montréal site was sampled once in July 1994. All unionids, including empty shells, were removed by hand from a 1-m^2 polyvinyl chloride (PVC) quadrat randomly placed on the bottom substrate using self-contained underwater breathing apparatus (SCUBA). The upper 10 cm of sediment within the quadrat was probed by hand to locate living and recently dead individuals buried immediately beneath the surface. An underwater light was used to aid collections in areas of low visibility. We decided a priori to use five replicated quadrats at each site, since this was expected to yield a precision of approximately 20% when sampling unionid densities of 10–30 mussels/m^2 (Downing and Downing 1992). The sole exception to our sampling protocol was the Port of Montréal, where unionid and dreissenid densities were not sampled; living and recently dead unionids were randomly collected by SCUBA and provided by a local environmental consulting firm (Subdev Canada Inc.).

Dreissena became established in the upper St. Lawrence River ca. 1990 (Griffiths et al. 1991); settled mussels, including adults, were present in Lake St. Louis and Lake St. François in the spring of 1991 (A. Ricciardi, personal observation). Dreissenid densities were estimated using SCUBA and randomly placed 1-m^2 quadrats (at least five replicates) at the Lake St. Louis and Lake St. François sites, since preliminary surveys (in 1992) showed that these sites had relatively small *Dreissena* populations (10^2/m^2). Smaller (25 × 25 cm, or 0.0625-m^2) quadrats were used at the Soulanges Canal sites, where dreissenid densities were on the order of 10^3/m^2. Objects with attached mussels were removed from quadrats placed at sites in Lake St. Louis, Lake St. François, and the west section of the Soulanges Canal. In the east section of the Soulanges Canal, where the bottom substrate is predominantly mud, quadrats were placed on the concrete canal walls at 3–5 m depths and dreissenids were scraped into bags by a SCUBA diver using a knife. In the laboratory, dreissenids were removed from unionids and other substrates, using a knife and a bristle brush (for small specimens). All dreissenids were washed through a 1-mm mesh sieve and counted under a dissecting microscope. Data from sites that were sampled more than once during a year were averaged for that year.

Development of predictive models

Our analysis consisted of modelling the relationships between *Dreissena* density and infestation variables by three approaches. We first analyzed these relationships empirically with simple linear regression models using SAS procedures (SAS Institute Inc. 1988). Proportion data (i.e., colonized unionids; unionid mortality) were transformed as $\sin^{-1}(\text{proportion}^{0.5})$ to achieve a better linear fit. The remaining variables spanned two to four orders of magnitude in range (Table 2), and thus were $\log_{10}$-transformed to stabilize their variances and reduce the influence of extreme values (Zar 1984). Our second approach investigated the possibility that the colonization of unionids by dreissenids is a simple space-occupancy problem controlled by stochastic processes. We thus derived a model to predict unionid colonization on the basis of the Poisson distribution and fitted it to the percent colonization data using a nonlinear iterative regression technique (Wilkinson 1989). We verified this model by testing (*i*) its ability to predict the proportion of unionids colonized by *Dreissena*, and the mean infestation intensity, and (*ii*) the expected 1:1 correspondence between mean infestation and variance required for a simple Poisson distribution (Zar 1984). Our analysis led us to consider a third approach in which we fitted a compound Poisson model (Thomas 1949) that accounted for the tendency of dreissenid mussels to aggregate and form clusters on unionid shells.

Estimating unionid surface area

In the process of developing our simple Poisson model, we needed to determine the allometric relationship between unionid shell length (cm) and surface area (cm^2). To do this, we randomly selected 50 unionids from the Lake St. Louis and Soulanges Canal collections. The surface area of each unionid was estimated by spreading a sheet of aluminum foil over the entire shell, subsequently weighing the foil, and multiplying this weight by an area-to-weight ratio determined from sample masses of foil. The maximum length of the shell was measured to the nearest millimetre, using dial callipers. The $\log_{10}$-transformed shell length and surface area variables were related by linear regression (SAS Institute Inc. 1988). This equation permitted us to estimate the surface area available for colonization by *Dreissena*, using data from unionids in the Great Lakes – St. Lawrence River system.

An indicator of mortality: the proportion of dead unionids in a population

Data on the proportion of dead unionids in populations within the Great Lakes-St. Lawrence River system comprised a second data set (Table 3) that was used to determine if *Dreissena* density and infestation intensity are significant predictors of unionid mortality. We considered a high proportion of recently dead unionids in a population to indicate relatively high mortality, since we found few studies that provided a direct measure of mortality. A similar measure, the ratio of live to dead unionids, was used in other studies as an indicator of increased mortality as a result of *Dreissena* fouling in Lake St. Clair (Hunter and Bailey 1992), western Lake Erie (Haag et al. 1993), and the Detroit River (Ohnesorg et al. 1993). An increase in the proportion of dead unionids was correlated with both a decrease in living unionid density and an increase in *Dreissena* density across sites in Lake St. Clair (Hunter and Bailey 1992). Therefore, we chose to use this proportion as an indicator of unionid mortality to investigate

Table 1. Field data used in the analysis.

Site	*Dreissena* density (no./m^2)	Unionid density (no./m^2)	% of unionids colonized	Mean no. of *Dreissena* per unionid	Max. no. of *Dreissena* per unionid	Sources of data
St. Lawrence River						
Soulanges Canal						
East site, 1992	1 990 (384)	21.0 (3.4)	74	3.1 (0.6)	12	This study; Ricciardi 1994
East site, 1993	1 819 (283)	15.0 (4.7)	95	9.9 (0.9)	75	This study; Ricciardi 1994
East site, 1994	3 712 (247)	3.0 (1.7)	100	19.6 (6.0)	61	This study
West site, 1994	2 944 (539)	5.3 (3.4)	100	43.8 (9.2)	134	This study
Lake St. Louis-1, 1992	101 (21)	19.2 (4.0)	58	0.8 (0.2)	4	This study
Lake St. Louis-2, 1992	123 (28)	48.0 (9.2)	59	1.3 (0.4)	6	This study
Lake St. Louis-2, 1994	851 (307)	48.6 (16.0)	62	8.7 (3.8)	92	This study
Lake St. François, 1992	165 (39)	120.5 (16.0)	55	1.2 (0.04)	9	This study
Port of Montréal, 1994			100	23.1 (2.8)	42	This study
Laurentian Great Lakes						
Lake St. Clair-2	48.0	5.7	70	2.3		Hebert et al. 1989
Lake St. Clair-3			87	4.3		Hebert et al. 1989
Lake St. Clair-4			47	1.4		Hebert et al. 1989
Lake St. Clair-5			60	1.9		Hebert et al. 1989
Lake St. Clair-7	195.0	11.3	90	8.2	38	Hebert et al. 1989
Lake St. Clair-8			92	17.1		Hebert et al. 1989
Lake St. Clair-9			73	1.7		Hebert et al. 1989
Lake St. Clair-10			93	3.9		Hebert et al. 1989
Lake St. Clair-13	6 000.0			5496.0	10 520	Griffiths 1993; Hebert et al. 1991
Lake St. Clair-Puce	5 000.0	1.7	100	642.0	1 991	Griffiths 1993; Gillis and Mackie 1994
Lake Erie-Presque Ile			100	234.0		Mastellar and Schloesser 1992
Western L. Erie	15 000.0		100	216.0		Haag et al. 1993; Garton and Haag 1993; J.R. Hageman[a]
Monroe Canal	700 000.0			6777.0	10 732	Schloesser and Kovalak 1991
Mississippi River Basin						
Peoria	1.2	12.0	10	0.1		Tucker et al. 1993
LaGrange	1.2	6.4	6	0.1		Tucker et al. 1993
Alton	7.3	8.2	27	0.6		Tucker et al. 1993
Lake Swan-outflow	0.3	12.9	2			Tucker et al. 1993
Lake Swan-interior	2.7	8.7	20			Tucker et al. 1993
Grafton	1.5	4.9	27	0.3		Tucker et al. 1993
Piasa Creek	1.1	2.3	18	0.3		Tucker et al. 1993
Mile 217			100	37.3	219	Tucker 1994

Table 1 (*concluded*).

Site	*Dreissena* density (no./m²)	Unionid density (no./m²)	% of unionids colonized	Mean no. of *Dreissena* per unionid	Max. no. of *Dreissena* per unionid	Sources of data
Mazurian Lakes, Poland						
Lake Mikolajskie, 1972	700.0	0.4	85	20.0	99	Lewandowski 1976; Stanczykowska 1975; Stanczykowska et al. 1976
Lake Mikolajskie, 1974	1 000.0		92	52.0	132	Lewandowski 1976
Lake Beldany	25.0				40	Lewandowski 1976
Lake Jagodne	125.0				80	Lewandowski 1976
Lake Sniardwy	425.0				85	Lewandowski 1976
Lake Niegocin	1 300.0				186	Lewandowski 1976

Note: Values in parentheses for St. Lawrence River sites are standard errors.
[a]J.R. Hageman, F.T. Stone Laboratory, Put-in-Bay, Ohio, personal communication.

its correlation with *Dreissena* abundance and infestation across a number of different habitats. Living and recently dead unionids (distinguished from older dead shells by the presence of mussel tissue or an intact ligament, and by the absence of severe shell erosion) were obtained from five sites on the St. Lawrence River (Lake St. Louis, Lake St. François, two sections of the Soulanges Canal, and the Port of Montréal), and these data were supplemented by similar data from the North American literature (Hebert et al. 1991; Hunter and Bailey 1992; Haag et al. 1993; Gillis and Mackie 1994) (Table 3).

We recognize that a simple measure of the proportion of recently dead unionids in a population is not as meaningful an indicator of mortality as the change in unionid density over time, but there is a paucity of data concerning these density changes in the literature. Our previous experiences in sampling unionid populations in rivers and inland lakes throughout southwestern Quebec suggested that the proportion of dead unionids in populations occupying relatively pristine habitats (e.g., many southwestern Quebec lakes), or even habitats that are subject to some perturbation (e.g., the lower Ottawa River), is usually well below 10%. This is considerably lower than the proportions recorded in habitats invaded by *Dreissena* (Table 3). Therefore, we assumed that if *Dreissena* density and infestation were strong correlates of unionid mortality, then we would be able to detect these relationships using our surrogate variable.

Results and discussion

Empirical relationships between infestation and *Dreissena* field density

The proportion of unionids colonized by *Dreissena* at a given site is strongly dependent on the density of the *Dreissena* population at that site ($r^2 = 0.90$, $p < 0.0001$) and follows a saturation curve that increases rapidly with *Dreissena* density up to ca. 200/m^2, where it plateaus at 70–80% colonization (Fig. 1). Typically, over 90% of unionids are colonized when *Dreissena* densities reach 10^3 mussels/m^2.

The mean number of dreissenids on each unionid (mean infestation intensity) is strongly correlated with *Dreissena* field density (Fig. 2; Table 4), which accounts for 81% of the variance. This relationship is equally applicable to lentic and lotic habitats (analysis of covariance (ANCOVA), $F = 1.85$, $p > 0.19$), although infestation intensities tended to be lower in lotic situations. The maximum number of *Dreissena* attached to a unionid (maximum infestation intensity) at a given site is also correlated with *Dreissena* field density ($r^2 = 0.58$, $p < 0.0001$), but is significantly lower in lotic situations (ANCOVA, $F = 11.27$, $p < 0.005$; Fig 3), which may reflect the greater availability of alternative hard substrates in running waters.

The mean infestation intensity remains low until the majority of unionids in a population is colonized (Fig. 4). Unionids are then subject to rapid increases in infestation (Table 5), possibly as a result of (*i*) the attraction of larvae and young-of-the-year to established mussel clusters on unionids (gregarious settlement), or (*ii*) self-recruitment by unionid-bound dreissenid populations. In both cases,

Table 2. Ranges and mean values of field data in Table 1.

Variable	Range	Mean ± SE	Median	*n*
Dreissena field density	0.3 – 700 000	27 464 ± 25 874	195.0	27
Unionid density	0.4 – 120.5	18.9 ± 6.3	8.7	19
% unionids colonized	2.0 – 100	66.7 ± 6.0	73.5	30
Mean no. of *Dreissena* per unionid	0.1 – 6777	454.3 ± 285.6	6.3	30
Max. no. of *Dreissena* per unionid	4.0 – 10 732	1227.9 ± 725.2	82.5	20

Table 3. Data on unionid mortality, with associated infestation intensity and zebra mussel density from sites in the Great Lakes – St. Lawrence River system.

Site	*Dreissena* density (no./m^2)	No. of *Dreissena* per unionid	Proportion of dead unionids	Reference
Lake St. Clair (west)	152		3.8	Hunter and Bailey 1992
Lake St. Clair (central)	2 847		52.6	Hunter and Bailey 1992
Lake St. Clair (east)	11 655	c. 5500	98.0	Hunter and Bailey 1992; Hebert et al. 1991
Lake St. Clair (Puce)	5 000	642	98.4	Gillis and Mackie 1994
Lake Erie (Put-in-Bay)		216	32.4	Haag et al. 1993
Lake Erie (Kelley's Island)		216	43.2	Haag et al. 1993
Detroit River	c. 5 000		90.0	Ohnesorg et al. 1993
Lake St. François, 1992	165	1.2	14.7	This study
Lake St. Louis, 1992	123	1.3	27.3	This study
Port of Montréal, 1994		23.1	39.0	This study
Soulanges Canal (east), 1992	1 990	3.1	16.6	This study
Soulanges Canal (east), 1993	1 819	9.9	25.0	This study
Soulanges Canal (east), 1994	3 712	19.6	57.0	This study
Soulanges Canal (west), 1994	2 944	43.8	60.0	This study

larval settlement is enhanced by the increased surface area provided by dreissenid shells themselves (Mackie 1990); thus, the rate of infestation should increase over time. However, during initial colonization, the rate of infestation should be limited by the low abundance of larvae in the water column, i.e., infestation levels should be dependent on factors influencing larval settlement. The initial colonization of unionids by *Dreissena* in the Illinois and Mississippi rivers consisted primarily of single attachments, and larger unionids were more likely than smaller specimens to bear attached *Dreissena* (Tucker et al. 1993); during subsequent colonization, infestation varied exponentially with unionid shell length (Tucker 1994). At low infestation rates, unionid shell length explained 19% of the variance in the number of *Dreissena* attached to unionids in the upper St. Lawrence River (A. Ricciardi, in preparation), between 23% (Mackie 1990) and 43% (Hebert et al. 1989) for unionids in the Great Lakes, and as much as 97% for unionids in the upper Mississippi River (Tucker 1994).

Predicting infestation from a Poisson model

We attempted to fit a stochastic model to the data on the basis of the null hypothesis that the colonization of unionids by dreissenid mussels, both as settling larvae and as migrating young-of-the-year mussels, is a process characterized by a large element of chance or randomness. We assumed that the exposed surface area on a unionid shell contains a large number (n) of locations that can be occupied by a byssally attached dreissenid, and that each of these locations has the same probability (p) of being occupied. The probability that exactly r of these locations will be occupied is described by the binomial distribution

$$[1] \quad P_{k=r} = (n!/(r!(n - r)!))\, p^r\, (1 - p)^{n-r}$$

Let us assume that np (the mean of the binomial distribution) can be represented as a linear function of the overall dreissenid density, D (number of mussels per square metre), in the environment containing the unionids. We can express this function as

$$[2] \quad np = \mu s D$$

where s is the mean colonizable space (in m^2) available on each unionid, and μ is a measure of the preference of *Dreissena* for this space, relative to other available substrate in the surrounding habitat. Assuming also that n is very large, p is small, np is of moderate magnitude, and r is negligible compared with n, then the probability of

Table 4. Linear regression models used to predict infestation and impact on unionids.

	r^2	p	n	SE_{est}
$\log_{10}(\text{avginfest}) = 0.812 \log_{10}(\text{density}) - 1.073$	0.807	<0.0001	21	0.630
$\sin^{-1}(\text{pcol}^{0.5}) = 0.302 \log_{10}(\text{density}) + 0.332$	0.902	<0.0001	21	0.150
$\log_{10}(\text{maxinfest}) = 0.751 \log_{10}(\text{density})$	0.584	<0.0001	18	0.641
$\sin^{-1}(\text{pmort}^{0.5}) = 0.498 \log_{10}(\text{density})$	0.644	<0.0029	11	0.269
$\sin^{-1}(\text{pmort}^{0.5}) = 1.350 \log_{10}(\text{density}) - 3.858$[a]	0.815	<0.0021	8	0.181
$\sin^{-1}(\text{pmort}^{0.5}) = 0.262 \log_{10}(\text{avginfest}) + 0.363$	0.692	<0.0015	11	0.213

Note: avginfest, mean no. of *Dreissena* per unionid; maxinfest, maximum no. of *Dreissena* per unionid; density, *Dreissena* field density (no./m^2); pcol, proportion of unionids colonized by *Dreissena*; pmort, proportion of dead unionids in a population.

[a]Excluding *Dreissena* densities < 1000/m^2.

Table 5. Percent increases in *Dreissena* infestation of unionids.

Site	Year	Percentage of unionids colonized	Mean no. of *Dreissena* per unionid	% increase in infestation	Reference
Lake Erie (east)	1990	100	121		Mastellar and Schloesser 1992
	1991	100	234	93	Mastellar and Schloesser 1992
Lake Mikolajskie (Poland)	1972	85	20		Lewandowski 1976
	1974	92	52	160	Lewandowski 1976
Soulanges Canal (east site)	1992	74	3.1		Ricciardi 1994
	1993	95	9.9	219	Ricciardi 1994
Lake St. Clair (Puce, Ont.)	1989	c.100	143		Gillis and Mackie 1994
	1990	c.100	642	349	Gillis and Mackie 1994

r locations being occupied (i.e., r dreissenids on a unionid) is given by

[3] $$P_{k=r} = (1/r!)\,(\mu sD)^r\,(1 - \mu sD/n)^n \approx (1/r!)\,(\mu sD)^r\,e^{-\mu sD}$$

Equation 3 is the Poisson distribution (Zar 1984) with a mean and variance equal to μsD, which is the expected infestation per unionid. We estimated s using our allometric regression equation relating surface area to shell length for St. Lawrence River unionids:

[4] $$\log_{10}(\text{surface area}) = 1.981 \log_{10}(\text{shell length})$$

$$r^2 = 0.92,\ \text{SE} = 0.053$$

Assuming a mean unionid shell length of 9.5 cm (on the basis of the combined data from Mackie 1990, Schloesser and Kovalak 1991, and this study), and correcting for back-transformation bias, eq. 4 gives us a mean surface area of 87.7 cm^2. In most cases, only the posterior region of a unionid (partially buried in sediment) is available for *Dreissena* colonization (Mackie 1990; Schloesser and Kovalak 1991; Hunter and Bailey 1992; Haag et al. 1993; A. Ricciardi, personal observation), hence we estimate an exposed surface area (s) of approximately 44 cm^2 (0.0044 m^2). Our Poisson null model then predicts the proportion of uncolonized unionids ($P_{k=0}$) to be

[5] $$e^{-0.0044\mu D}$$

and the proportion colonized to be

[6] $$1 - e^{-0.0044\mu D}$$

We tested the fit of this model by using nonlinear regression (Wilkinson 1989) and found it to be nearly as effective ($r^2 = 0.78$) as our previously determined empirical model (Table 3) at predicting the proportion of colonized unionids from *Dreissena* field density. The estimated value for the preference parameter (μ) obtained from this nonlinear fit was 2.2 (95% C.I. = 1.2–3.2), which suggests that *Dreissena* (primarily *D. polymorpha*) is about twice as likely to colonize unionids as other substrates in the surrounding habitat, and thus corroborates laboratory and field observations of the preferential colonization of unionids by *Dreissena* (Biryukov et al. 1964; Wolff 1969; Lewandowski 1976; Mackie 1990; Ricciardi 1994). The predicted mean infestation per unionid (μsD) becomes $0.0097D$, and we obtain the following relationship:

[7] $$\text{Predicted colonization} = 1 - e^{-0.0097D}$$

$$r^2 = 0.783,\ \text{SE}=0.032$$

This model was further tested by comparing predicted and observed mean infestations for given values of *Dreissena* field density, D. We found that the model provides useful rough estimates, but it generally underestimates mean infestation intensities, probably because it does not account for the effect of contagious infestation. The relationship between the mean infestation and variance suggests that dreissenids are contagiously distributed on unionids (Fig. 5) and that our simple Poisson model, although useful as a basis for

Fig. 1. Proportion of unionids colonized by *Dreissena* versus *Dreissena* field density over the range 0–1000/m^2; values greater than 1000/m^2 converge to 100% colonization (Table 1) and are omitted for clarity. Solid circles denote observed values; open circles denote values predicted by the compound Poisson model (eq. 14).

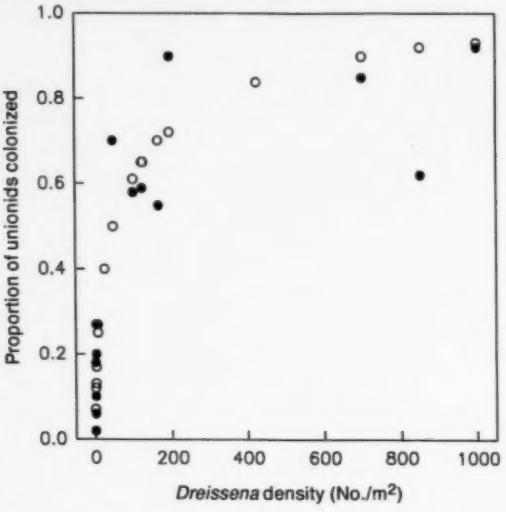
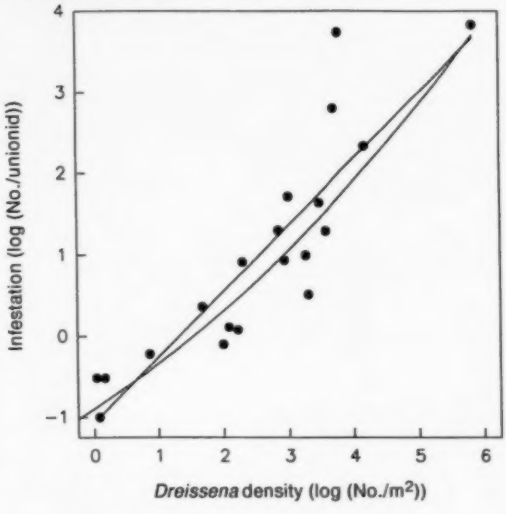


Fig. 2. Mean infestation intensity versus *Dreissena* field density (both variables are $\log_{10}$-transformed). Curved line denotes infestation predicted by the compound Poisson model (eq. 14); straight line denotes infestation predicted by linear regression model (Table 4). Points represent observed values from Table 1.



further modelling, is inappropriate in its current form to accurately describe infestation patterns.

Using a compound Poisson model to predict infestation

Analysis of variance-to-mean ratios for unionid-bound dreissenids in the St. Lawrence River indicated that young-of-the-year dreissenids are more contagiously distributed than adult dreissenids (Table 6). Furthermore, young-of-the-year dreissenids tend to aggregate around adult (1- and 2-year-old) dreissenids and thus form structured clusters on unionid shells (A. Ricciardi, personal observation). We therefore fitted a compound Poisson model (Thomas 1949) to account for this clustering tendency. The model is based on two parameters: λ, which describes the Poisson distribution of adult dreissenids on unionid shells, and β, which describes the distribution of young-of-the-year dreissenids around adults. The probability of k dreissenids on a unionid, $P(k)$, is given by the following equation adapted from Thomas (1949):

$$[8] \quad P(k) = \sum_{r=1}^{k} (\lambda^r e^{-\lambda} / r!)(r\beta)^{k-r} e^{-r\beta} / (k - r)!)$$

The mean infestation per unionid is given by

$$[9] \quad \lambda(1 + \beta)$$

and the variance is given by

$$[10] \quad \lambda(1 + 3\beta + \beta^2)$$

We calculated λ and β for each record in our data set that contained mean and variance estimates (n = 17), $\log_{10}$-transformed both parameters, and then related them to *Dreissena* density (D) by linear regression. Backtransformation of the regression equations produced the following power functions:

$$[11] \quad \lambda = 0.119D^{0.453} \quad r^2 = 0.69, p < 0.002, \text{SE} = 2.37$$

$$[12] \quad \beta = 0.103D^{0.5} \quad r^2 = 0.50, p < 0.018, \text{SE} = 26.7$$

The predicted proportion of colonized unionids is thus given by

$$[13] \quad 1 - e^{-\lambda}$$

where λ is derived from eq. 11. After fitting both eq. 11 and eq. 12 into eq. 9, we obtain the following:

[14] Predicted mean infestation =

$$0.119D^{0.453}(1 + 0.103D^{0.5})$$

We tested eq. 13 and eq. 14 on our entire data set and found that they performed better than equations from the previous Poisson model and explained similar proportions of variance in percent colonization (r^2 = 0.89, $p < 0.0001$; Fig. 1) and infestation intensity (r^2 = 0.82, $p < 0.0001$; Fig. 2), respectively, as our empirical models. The compound Poisson model may also be used to predict the number of unionids having a given level of infestation using eq. 8; thus, the number of unionids with infestations exceeding a critical threshold, c, may be estimated by calculating $P(k \geq c)$.

Can dreissenid density and infestation be used to predict unionid mortality?

Some studies have linked an increase in the proportion of dead unionids and a decline in living unionid density with an increase in dreissenid density (Hunter and Bailey 1992;

Haag et al. 1993; Ohnesorg et al. 1993). We have confirmed these relationships for the unionid population in the Soulanges Canal (Fig. 6). Furthermore, linear regression analysis shows that *Dreissena* density explains 64% (82% for densities > 10^3 mussels/m^2; Fig. 7), and mean infestation intensity explains 69% (Fig. 8), of the variability in the proportion of dead unionids in populations across the Great Lakes – St. Lawrence River system. These results corroborate previous studies that correlated significant increases in unionid mortality (declines in unionid density) with increases in local *Dreissena* abundance, both temporally (Arter 1989; Gillis and Mackie 1994) and spatially within a habitat (Hunter and Bailey 1992; Ohnesorg et al. 1993). Infestation intensity would probably explain an even greater amount of the variance in unionid mortality if the size structure (biomass) of attached dreissenids is considered. Haag et al. (1993) hypothesized that a unionid suffers an energy loss in maintaining its proper orientation in the substrate under the destabilizing weight of dreissenids concentrated on its posterior shell; a cluster of large dreissenids may therefore have a greater impact than the same number of smaller (e.g., young-of-the-year) mussels.

The variance in unionid mortality that is explained by *Dreissena* is remarkable, given that much of the decline of native freshwater mussels during the past century has been attributed to habitat destruction from impoundment, erosion, channelization, and contaminants (see Williams et al. 1993 for review). For example, a decline in water quality coupled with periodically low oxygen levels is the hypothesized cause of the long-term reduction of a rich unionid population in western Lake Erie (Nalepa et al. 1991*b*). However, although water quality in the Great Lakes has generally improved in recent years following phosphorus abatement (Great Lakes Water Quality Board 1987; Nicholls and Hopkins 1993), high mortality and local extinction of unionid communities have recently occurred in western Lake Erie (Haag et al. 1993), eastern Lake Erie (Maleski and Masteller 1994), Lake St. Clair (Hunter and Bailey 1992; Gillis and Mackie 1994), the Detroit River (Ohnesorg et al. 1993), and the upper St. Lawrence River (this study), wherever high densities of *Dreissena* have become established. Therefore, the introduction of *Dreissena* may be the critical stress that causes the extirpation of threatened unionid populations throughout most of North America.

Since habitat characteristics may be used to predict dreissenid densities (Ramcharan et al. 1992; Mellina and Rasmussen 1994), they may also indirectly predict unionid impacts. Impacts should therefore be maximal in lentic habitats with high pH, high calcium concentrations, and low phosphate concentrations, i.e., habitats that typically support high densities of *Dreissena* (Ramcharan et al. 1992; Mellina and Rasmussen 1994). These limnological variables may also prove useful in predicting infestation intensities on unionids, including the critical thresholds that precede significant population declines. At present, there are few available data from which the density and infestation thresholds that cause mortality may be accurately determined. Although minor impacts such as shell deformities have been reported at mean infestations as low as 20 dreissenids/unionid (Lewandowski 1976), heavy mortality and extirpations in lakes are often associated with mean infestations on the order of 10^2/unionid. Significantly reduced survival was observed in Lake Erie populations having a mean infestation of 216/unionid (Haag et al. 1993), and a mean infestation of 642/unionid preceded the extirpation of unionids at a site in Lake St. Clair (Gillis and Mackie 1994). Hundreds of attached zebra mussels

Fig. 3. Maximum infestation intensity versus *Dreissena* field density (both variables are $\log_{10}$-transformed). Solid circles denote lentic habitats ($Y = 1.095X$, $r^2 = 0.69$, $p < 0.001$); open circles denote lotic habitats ($Y = 0.880X - 1.202$, $r^2 = 0.91$, $p < 0.005$). Regression lines are significantly different (ANCOVA, $p < 0.005$).

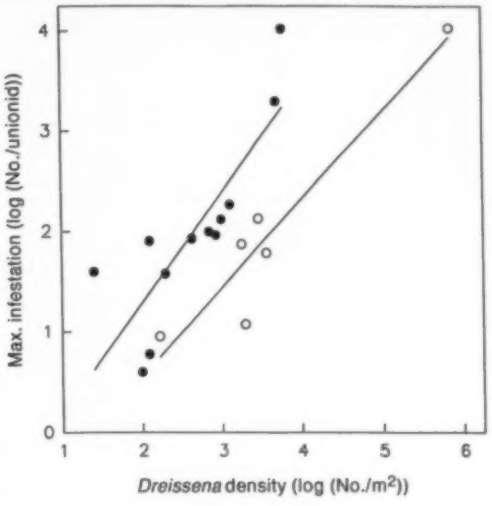


Fig. 4. Mean infestation intensity plotted against the percentage of unionids colonized by *Dreissena*.

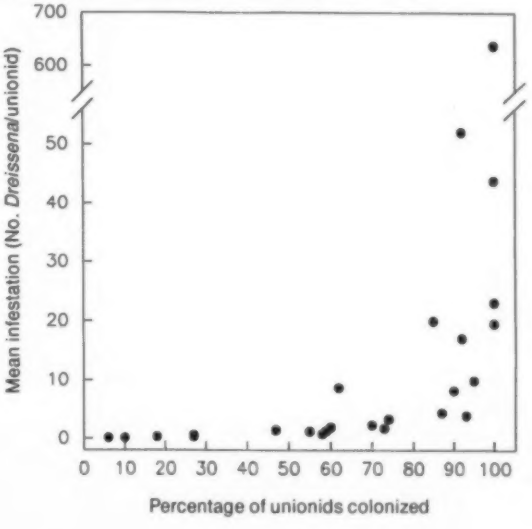


Fig. 5. Variance versus mean infestation intensity (both variables are $\log_{10}$-transformed). Solid line represents 100% correspondence between mean and variance.

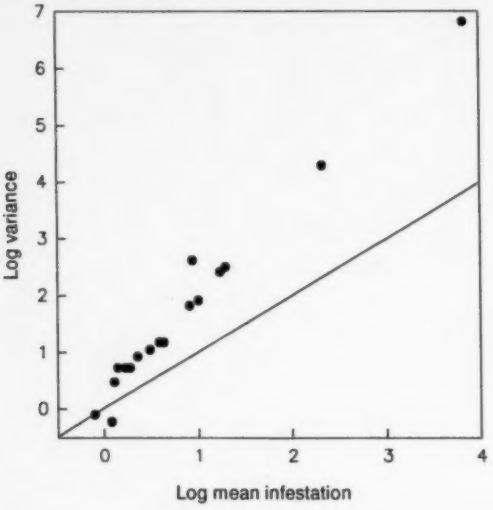


Table 6. Variance to mean ratios for young-of-the-year (YOY) and adult dreissenids attached to unionids (n = 146) in the upper St. Lawrence River.

	Mean number per unionid, m	Variance, s^2	s^2/m
YOY dreissenids	3.2	46.9	14.7
Adult dreissenids	4.9	18.3	3.7

Note: A contagious distribution is indicated by values of $s^2/m > 1$ (Elliott 1977).

were found on unionids in Lake Balaton, Hungary (Sebestyen 1935, cited in Lewandowski 1976), less than 2 years before the unionid population suffered a major decline (Wagner 1936; Sebestyen 1938). However, some evidence suggests that, at least for some unionid populations, the mortality threshold is much lower than that which has been observed for these large lentic habitats. Very few unionids from our upper St. Lawrence River sites were found alive with infestations exceeding 100 dreissenids/unionid, even though a large number of dead unionids were found with these infestation levels (A. Ricciardi, personal observation); a sharp increase in mortality among unionids in Soulanges Canal occurred when the mean infestation reached 20/unionid (Fig. 6), at a zebra mussel field density near 4000/m^2. Unionid mortality increased noticeably in a small inland lake when the mean infestation exceeded 70/unionid at a *Dreissena* density near 1000/m^2 (Garton 1994; D.W. Garton, Indiana University, Kokomo, Ind. 46904-9003, U.S.A, personal communication). When we excluded sites with densities less than 1000/m^2, we obtained a much stronger correlation (r^2 = 0.815, p < 0.0021) between mortality and *Dreissena* density (Fig. 7), suggesting that mortality sharply increases at *Dreissena* densities above 1000/m^2. According to this model, unionid mortality greater than 90% is associated with *Dreissena* densities exceeding 6000/m^2. The mean and maximum infestation intensities are near 100/unionid and 700/unionid, respectively, at these densities (Fig. 2). Therefore, a *Dreissena* density of 1000/m^2 appears to be a critical threshold above which unionid mortality increases significantly with *Dreissena* density until the population becomes virtually extirpated at a density and mean infestation intensity of approximately 6000/m^2 and 100/unionid, respectively. These critical values probably vary according to the size structure of attached dreissenids and the species composition of the unionid population.

Unionid morphologies and behaviours (e.g., burrowing activity) that are intrinsic to gender or species may potentially enhance or reduce fouling, and thus cause differential impacts within a unionid population (Haag et al. 1993). In Europe, *Dreissena* occurs more frequently and in greater numbers on *Anodonta* shells than on *Unio* shells (Kuchina 1964; Lewandowski 1976; Arter 1989), probably because *Unio* is almost completely buried in its natural position in the substrate and thus provides little surface area for colonization, whereas *Anodonta* normally exposes a large portion of its shell (Arter 1989). In the Mississippi River, unionids are differentially colonized; thick-shelled, ornamented species are more heavily colonized than thin-shelled, unornamented species (Tucker 1994). Species-specific and sex-specific differences in impacts and survival are likely to become significant after infestation levels rise (Haag et al. 1993). Differences in mortality among infested species have already been observed in Lake St. Clair (Hunter and Bailey 1992; Gillis and Mackie 1994) and Lake Erie (Haag et al. 1993).

In habitats that support *Dreissena* densities of at least 1000/m^2, virtually all unionids become infested in 2–3 years, as found in Lake St. Clair (Gillis and Mackie 1994), the Detroit River (Ohnesorg et al. 1993), eastern Lake Erie (Masteller and Schloesser 1992), the upper Mississippi River (Tucker 1994), and the upper St. Lawrence River (Ricciardi 1994). High infestation and heavy mortality may occur shortly thereafter, if the local dreissenid density continues to rise. Large numbers of dead unionids were found washed up on shore, and unionid populations declined noticeably, less than 5 years after *Dreissena* invaded Lake Balaton (Wagner 1936; Sebestyen 1938). Severe (90–100%) reductions in unionid density were recorded in Lake St. Clair (Gillis and Mackie 1994) and the Detroit River (Ohnesorg et al. 1993) approximately 4 years after *Dreissena* invaded these habitats. Similarly, an 83% decline in unionid density in Presque Isle Bay, Lake Erie, occurred 3 years after the establishment of a *Dreissena* population (Maleski and Masteller 1994). The unionid population around Kelley's Island in western Lake Erie was virtually eliminated 5 years after *Dreissena* invaded the region (J. R. Hageman, F.T. Stone Laboratory, Put-in-Bay, Ohio, 43456-0119, U.S.A., personal communication). Unionid communities in the upper St. Lawrence River appear to be following the same pattern; in the Soulanges Canal, unionid density has varied inversely with *Dreissena* density over time and the population is on the verge of

Fig. 6. (A) Changes in the density of living unionids and the percentage of dead unionids in the population at the Soulanges Canal (east site), 1992–1994. (B) Changes in *Dreissena* infestation intensity on unionids over this same time period.

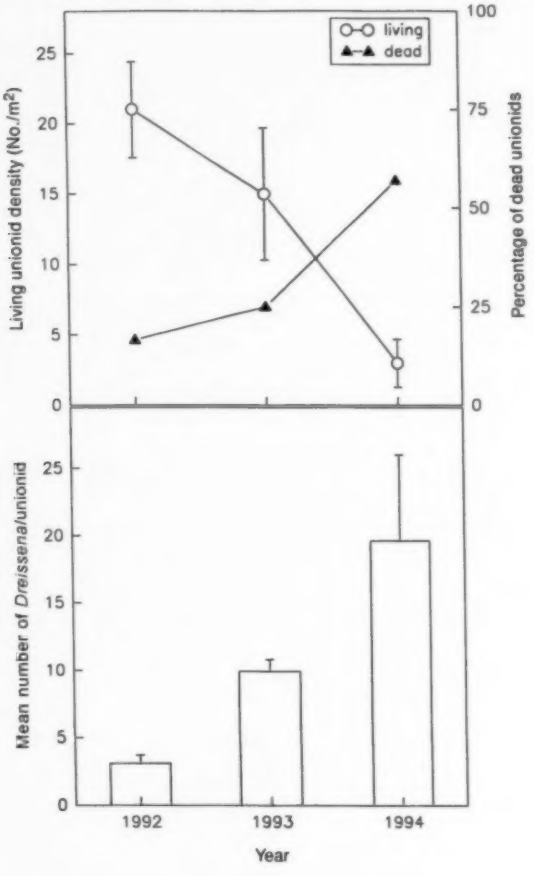


Fig. 7. Proportion of dead unionids in a population ($\sin^{-1}x^{0.5}$ transformed) versus *Dreissena* field density ($\log_{10}$-transformed). Line denotes $Y = 1.350X - 3.858$.

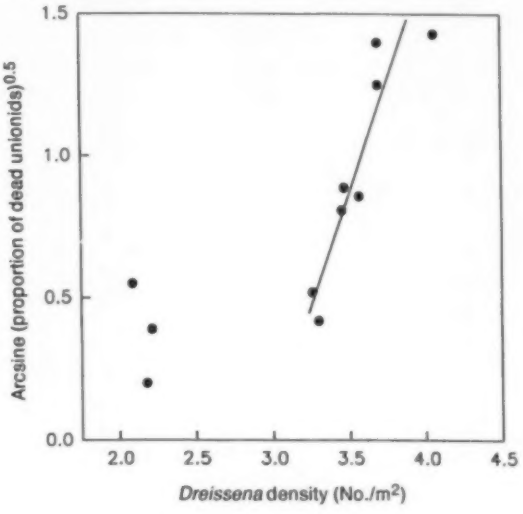
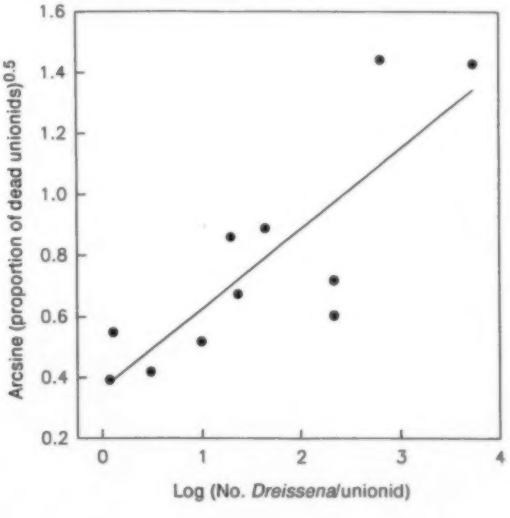


Fig. 8. Proportion of dead unionids in a population ($\sin^{-1}x^{0.5}$ transformed) versus infestation intensity ($\log_{10}$-transformed): $Y = 0.262X + 0.363$.



extirpation, 4 years after *Dreissena* became established in that section of the river (A. Ricciardi, in preparation). These data suggest that the extirpation of a unionid population will occur within 4–5 years of a *Dreissena* invasion, provided that the *Dreissena* population grows to sufficient levels (>6000/m^2). Viable unionid populations in North America may ultimately be restricted to softwater habitats or geographic regions that are either invulnerable to *Dreissena* invasion or support very low densities of dreissenids (Strayer 1991; Ramcharan et al. 1992; Mellina and Rasmussen 1994).

Conclusions

Our study demonstrates that the infestation of unionids by *Dreissena* follows a very predictable pattern with increasing dreissenid density. The proportion of unionids colonized by *Dreissena* follows a saturation curve with rapid colonization at *Dreissena* densities up to 200/m^2. Dreissenids aggregate preferentially on unionids, forming a cluster whose size is correlated with the total population density of *Dreissena* in the habitat. These infestations may be accurately described by a compound Poisson model that takes into account the clustering tendency of young-of-the-year dreissenids. Unionid mortality (reflected by the proportion of recently dead unionids in a population) associated with these infestations varies strongly with the local *Dreissena* density. We predict sharply accelerated mortality at *Dreissena* densities above 1000/m^2, and heavy (>90%) mortality of unionids when the *Dreissena* density and mean

infestation intensity reach 6000/m^2 and 100 dreissenids/unionid, respectively. Extirpation of unionid populations will occur within 4–5 years after the establishment of *Dreissena* in habitats that support dreissenid densities of at least 6000/m^2. The general significance of these thresholds can be further tested as the *Dreissena* invasion of North American drainages continues and densities increase.

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References

Arter, H.E. 1989. Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland). Aquat. Sci. 51: 87–99.

Biryukov, I.N., M.Y. Kirpichenko, S.M. Lyakhov, and G.I. Segeeva. 1964. Living conditions of the mollusk *Dreissena polymorpha* Pallas in the Babinskii backwater of the Oka River. *In* B.K. Shtegman [ed.] Biology and control of *Dreissena*. Trudy Inst. Biol. Vnutr. Vod Akad. Nauk. SSSR, 7: 32–38.

Conn, D.B., and D.A. Conn. 1993. Parasitism, predation and other biotic associations between dreissenid mussels and native animals in the St. Lawrence River. *In* Proceedings of the Third International Zebra Mussel Conference, Toronto, Ont., February 23–26, 1993. *Edited by* J.L. Tsou. Electric Power Research Institute, Palo Alto, Calif.

Downing, J.A., and W.L. Downing. 1992. Spatial aggregation, precision, and power in surveys of freshwater mussel populations. Can. J. Fish. Aquat. Sci. 49: 985–991.

Elliott, J.M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. No. 25.

Fuller, S.L.H. 1974. Clams and mussels (Mollusca: Bivalvia), p. 215–273. *In* C.W. Hart and S.L.H. Fuller [ed.] Pollution ecology of freshwater invertebrates. Academic Press Inc., New York.

Garton, D.W. 1994. Impact of fouling by *Dreissena polymorpha* on unionids of Lake Wawasee, Indiana. *In* Abstracts of the Fourth International Zebra Mussel Conference, Madison, Wis., March 7–10, 1994. University of Wisconsin Sea Grant Institute.

Garton, D.W., and W.R. Haag. 1993. Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie, p. 111–128. *In* T.F. Nalepa and D.W. Schloesser [ed.] Zebra mussels: biology, impacts, and control. Lewis Publishers, Boca Raton, Fla.

Gillis, P.L., and G.L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Can. J. Zool. 72: 1260–1271.

Great Lakes Water Quality Board. 1987. Report on Great Lakes water quality to the International Joint Commission. IJC Great Lakes Regional Office, Windsor, Ont.

Green, R.H., R.C. Bailey, S.C. Hinch, J.L. Metcalfe, and V.H. Young. 1989. Use of freshwater mussels (Bivalvia: Unionidae) to monitor the nearshore environment of lakes. J. Great Lakes Res. 15: 635–644.

Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair, p. 414–437. *In* T.F. Nalepa and D.W. Schloesser [ed.] Zebra mussels: biology, impacts, and control. Lewis Publishers, Boca Raton, Fla.

Griffiths, R.W., D.W. Schloesser, J.H. Leach, and W.P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 48: 1381–1388.

Haag, W.R., D.J. Berg, D.W. Garton, and J.L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Can. J. Fish. Aquat. Sci. 50: 13–19.

Havlik, M.E. 1994. Are unionid translocations a viable mitigation technique? The Wolf River experience, Shawano, WI, August 1992 and August 1993. *In* Abstracts of the Fourth International Zebra Mussel Conference, Madison, Wis., March 7–10, 1994. University of Wisconsin Sea Grant Institute.

Hebert, P.D.N., B.W. Muncaster, and G.L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. 46: 1587–1591.

Hebert, P.D.N., C.C. Wilson, M.H. Murdoch, and R. Lazar. 1991. Demography and ecological impacts of the invading mollusc, *Dreissena polymorpha*. Can. J. Zool. 69: 405–409.

Hunter, R.D., and J.F. Bailey. 1992. *Dreissena polymorpha* (zebra mussel): colonization of soft substrata and some effects on unionid bivalves. Nautilus, 106: 60–67.

Imlay, M.J. 1982. Use of shells of freshwater mussels in monitoring heavy metals and environmental stresses: a review. Malacol. Rev. 15: 1–4.

Kasprzak, K. 1986. Role of Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the eutrophic Lake Zbechy and its outflow. Int. Rev. Gesamten Hydrobiol. 71: 315–334.

Kuchina, E.S. 1964. Distribution of the mollusk *Dreissena polymorpha* Pallas in the Northern Dvina River. *In* B.K. Shtegman [ed.] Biology and control of *Dreissena*. Trudy Inst. Biol. Vnutr. Vod Akad. Nauk. SSSR, 7: 25–31.

Lewandowski, K. 1976. Unionidae as substratum for *Dreissena polymorpha*. Pol. Arch. Hydrobiol. 23: 409–420.

Lewandowski, K., and A. Stanczykowska. 1975. The occurrence and role of bivalves of the family Unionidae in Mikolajskie Lake. Ekol. Pol. 23: 317–334.

Mackie, G.L. 1990. Early biological and life history attributes of the zebra mussel, *Dreissena polymorpha* (Bivalvia: Dreissenidae), and impacts on native bivalves in Lake St. Clair. p. 215–231. *In* Proceedings of the Technology Transfer Conference, Toronto, Ont., November 19–20, 1990.

Maleski, K.R., and E.C. Masteller. 1994. The current status of the Unionidae of Presque Isle Bay, Erie, PA. Bull. North Am. Benthol. Soc. 11: 109. [Abstr.]

Masteller, E.C., and D.W. Schloesser. 1992. Infestation and impact of zebra mussels on the native unionid population at Presque Isle State Park, Erie, PA. J. Shellfish Res. 11: 232. [Abstr.]

Mellina, E., and J.B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussels (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physico-chemical factors. Can. J. Fish. Aquat. Sci. 51: 1024–1036.

Nalepa, T.F., W.S. Gardner, and J.M. Malczyk. 1991*a*. Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. Hydrobiologia, 219: 239–250.

Nalepa, T.F., B.A. Manny, J.C. Roth, S.C. Mozley, and D.W. Schloesser. 1991*b*. Long-term decline in freshwater mussels (Bivalvia: Unionidae) of the western basin of Lake Erie. J. Great Lakes Res. 17: 214–219.

Nicholls, K.H., and G.J. Hopkins. 1993. Recent changes in Lake Erie (North Shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. J. Great Lakes Res. 19: 637–647.

Ohnesorg, K.L., R.D. Smithee, G.D. Longton, W.P. Kovalak, and D.W. Schloesser. 1993. Impact of zebra mussels (*Dreissena polymorpha*) on native mussels (Unionidae) in the Detroit River. *In* Abstracts of the Third International Zebra Mussel Conference, Toronto, Ont., February 23–26, 1993.

Ramcharan, C.W., D.K. Padilla, and S.I. Dodson. 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. Can. J. Fish. Aquat. Sci. 49: 2611–2620.

Ricciardi, A. 1994. Infestation and impacts of *Dreissena* on native unionids in the Upper St. Lawrence River. *In* Abstacts of the Fourth International Zebra Mussel Conference, Madison, Wis., March 7–10, 1994. University of Wisconsin Sea Grant Institute.

SAS Institute Inc. 1988. SAS/STAT user's guide. Release 6.03 edition. SAS Institute Inc., Cary, N.C.

Schloesser, D.W., and W. Kovalak. 1991. Infestation of unionids by *Dreissena polymorpha* in a power plant canal in Lake Erie. J. Shellfish Res. 10: 355–359.

Sebestyen, O. 1938. Colonization of two new fauna-elements of Pontus-origin (*Dreissena polymorpha* Pall. and *Corophium curvispinum* G.O. Sars *forma devium* Wundsch) in Lake Balaton. Verh. Int. Ver. Theor. Angew. Limnol. 8: 169–182.

Stanczykowska, A. 1975. Ecosystem of the Mikolajskie Lake. Regularities of the *Dreissena polymorpha* Pall. (Bivalvia) occurrence and its function in the lake. Pol. Arch. Hydrobiol. 22: 73–78.

Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Pol. Arch. Hydrobiol. 24: 461–530.

Stanczykowska, A., W. Lawacz, J. Mattice, and K. Lewandowski. 1976. Bivalves as a factor affecting circulation of matter in Lake Mikolajskie (Poland). Limnologica, 10: 347–352.

Strayer, D.L. 1991. Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. Can. J. Fish. Aquat. Sci. 48: 1389–1395.

Thomas, M. 1949. A generalization of Poisson's binomial limit for use in ecology. Biometrika, 36: 18–25.

Tucker, J.K. 1994. Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha*, in pool 26 of the Mississippi River. J. Freshwater Ecol. 8: 129–134.

Tucker, J.K., C.H. Theiling, K.D. Blodgett, and P.A. Thiel. 1993. Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (family Unionidae) in the upper Mississippi River system. J. Freshwater Ecol. 8: 245–251.

Wagner, H. 1936. Die Wandermuschel (*Dreissensia*) erobert den Platten-See. Nat. Volk, 66: 37–41.

Waller, D.L., J.J. Rach, W.G. Cope, and J.A. Luoma. 1993. A sampling method for conducting relocation studies with freshwater mussels. J. Freshwater Ecol. 8: 397–399.

Wiktor, J. 1963. Research on the ecology of *Dreissena polymorpha* Pall. in the Szczecin Lagoon (Zalew Szczecinski). Ekol. Pol. Ser. A, 11: 275–280.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Ill.

Williams, J.D., M.L. Warren, Jr., K.S. Cummings, J.L. Harris, and R.J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada. Fisheries, 18: 6–22.

Wolff, W.J. 1969. The Mollusca of the estuarine region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area. II. The Dreissenidae. Basteria, 33: 93–103.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall Inc., Englewood Cliffs, N.J. 718 p.

Zhadin, V.I., and S.V. Gerd. 1961. Fauna and flora of the rivers, lakes and reservoirs of the U.S.S.R. (Translated by A. Mercado, Israel Program for Scientific Translations, Jerusalem, 1963.)

Biogeographic patterns of fish species richness in Ontario lakes in relation to historical and environmental factors

Nicholas E. Mandrak

Abstract: Fish species richness in Ontario lakes was summarized for 80 equal-area quadrats and ranged from 59 species per quadrat in southwestern Ontario to 17 species per quadrat in northern Ontario. Correlograms based on Moran's *I* coefficient indicated the spatial structure of lake species richness was anisotropic and exhibited a strong south–north gradient of decreasing richness. Relationships among Euclidean distance matrices based on richness, postglacial dispersal, climate, elevation, lake chemistry, and lake morphometry were identified with the aid of the Mantel test and principal coordinates analysis. The presence of spatial autocorrelation may bias matrix correlations; therefore, spatial autocorrelation was removed using the partial Mantel test. The results of the partial Mantel test indicated regional lake species richness was significantly correlated with postglacial dispersal and climate. In particular, the results of principal coordinates analysis identified length of time since deglaciation, length of time covered by glacial lakes, distance from dispersal corridor, and mean annual air temperature as the dominant variables in these data sets.

Résumé : Nous avons fait le bilan de la richesse des lacs de l'Ontario en espèces de poissons, au moyen de 80 quadrats de superficie égale; cette richesse allait de 59 espèces par quadrat dans le sud-ouest de la province à 17 espèces dans le nord. Des corrélogrammes fondés sur le coefficient *I* de Moran indiquent que la structure spatiale de la richesse des lacs est anisotrope et présente un fort gradient sud–nord de diminution de la richesse. Nous avons établi les relations existant entre les matrices de distance euclidienne fondées sur la richesse, la dispersion post-glaciaire, le climat, l'altitude, la chimie du lac et la morphométrie du lac, à l'aide du test de Mantel et de l'analyse des coordonnées principales. Comme la présence d'une autocorrélation spatiale peut biaiser les corrélations matricielles, nous avons éliminé ce facteur en utilisant le test partiel de Mantel. Les résultats de ce test indiquent que la richesse des lacs à l'échelle régionale présente une corrélation significative avec la dispersion post-glaciaire et le climat. L'analyse des coordonnées principales a notamment permis d'identifier comme variables dominantes de ces séries de données le temps écoulé depuis la déglaciation, la durée de la période où la région était couverte de lacs glaciaires, la distance par rapport au couloir de dispersion et la température moyenne actuelle de l'air.

[Traduit par la Rédaction]

Introduction

Biogeographical analyses generally focus on identifying patterns in biological data and postulating processes that generate and maintain these trends. Patterns in species distributions are typically examined and compared with data representing hypothesized abiotic and biotic environmental processes. Both pattern and process variables may exhibit regular trends in space, that is, the values of a variable between sites are related as a result of the proximity of the sites to each other. This phenomenon is termed spatial autocorrelation. Spatial autocorrelation may result from spatially structured historical and environmental variables affecting species distributions, or it may be the result of extraneous variables not included in the study (Borcard et al. 1992). The presence of spatial autocorrelation violates the assumption of sample independence in traditional statistical analyses (e.g., correlation, regression; Bivand 1980; Legendre 1993). As a result, spatial autocorrelation is a confounding factor which may produce spurious correlations between pattern and process variables (Legendre 1990, 1993). These spurious correlations may overestimate the significance or the very presence of such interactions

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(Legendre and Troussellier 1988; Legendre 1990). Therefore, spatial autocorrelation should be examined to identify and remove spatial patterns prior to statistical testing (Borcard et al. 1992; Legendre 1993).

Patterns and processes may vary simultaneously over different scales (Levin 1992). Species richness is a product of a hierarchy of distribution patterns over a range of scales, and a hierarchy of processes structure these patterns (Ricklefs 1987). The choice of study scale may determine which processes appear to influence biogeographical patterns (Hinch 1991) as these patterns will generally match the scales of processes responsible for them (Ricklefs 1987). Traditionally, patterns in species richness have been examined at local and regional scales independently (Ricklefs 1987). It has been hypothesized that processes associated with abiotic (e.g., variation in physicochemical conditions), biotic (e.g., competition, predation), and stochastic factors structure local patterns; whereas, historical processes (e.g., dispersal, speciation) structure regional patterns (Ricklefs 1987; Tonn 1990). Ricklefs (1987) noted that "ecologists are beginning to accept that processes beyond their normal scale of consideration may influence structure and function of ecological systems."

Studies conducted at a local scale (i.e., between lakes within an area less than 1000 km^2, sensu Tonn 1990) have demonstrated the influence of lake size and pH (e.g., Harvey 1978, 1981; Somers and Harvey 1984; Eadie et al. 1986; Jackson and Harvey 1989; Minns 1989), and habitat heterogeneity (e.g., Eadie and Keast 1984) on fish species richness in Ontario lakes. At a regional scale (i.e., between lakes or drainage basins in an area greater than 1000 km^2 and less than 100 000 km^2), Matuszek and Beggs (1988) demonstrated the influence of lake area, pH, latitude (which may indicate spatial autocorrelation), elevation, and dissolved organic carbon on fish species richness. Radforth (1944), Jackson and Harvey (1989), and Minns (1989) hypothesized that regional patterns of fish species richness in Ontario may be related to postglacial dispersal and climate. However, none of these studies tested the relationships between regional richness and potential structuring processes such as postglacial dispersal and climate, nor the influence of spatial autocorrelation and scale on the results of the analyses.

In the present study, these relationships were tested and the influences of spatial autocorrelation and scale were assessed. The study was conducted at the regional scale, a scale generally neglected in aquatic studies (Hinch 1991). The objectives of the study were (1) to identify regional patterns of fish species richness in Ontario lakes; (2) to examine the relationships between richness and historical and environmental factors, controlling for the influence of scale and spatial autocorrelation; and (3) to postulate processes that influence observed patterns of regional lake species richness in Ontario.

Materials and methods

Species distribution data

The primary source of the biological data was the Fish Species Distribution Data System (FSDDS) of the Ontario Ministry of Natural Resources (OMNR). This data base contained 107 337 records for lakes and streams; one record represented the collection of a single species at a specific site on a given date. These records span the years from 1900 to 1992, although most of the FSDDS records were collected in OMNR lake and stream inventories between 1968 and 1985 (Mandrak and Crossman 1992*a*). Minns (1986) concluded that four game species were overrepresented in the OMNR Lake Inventory data, and Bowlby and Green (1987) found a positive correlation between median fork length and number of records, suggesting that smaller species (such as cyprinids) are underrepresented in the Lake Inventory data. An additional 21 878 records from published and unpublished sources, primarily for smaller species, were added to the data base in an attempt to reduce this bias. Therefore, the supplemented data base contained 129 215 records for 158 species and 5 subspecies. Approximately 88 500 records for 10 167 inland lakes in this data base were used in the current study. Because the distributions of introduced species may not have responded fully to the historical and environmental factors examined in this study, only 105 extant species native to inland lakes were used to estimate species richness. Species richness was measured as the total number of species recorded in each sampling unit. The richness data were standardized by log transformation ($\ln(x + 1)$) prior to further analyses.

Sampling unit selection

The selection of optimal sampling units is a problem common to biogeography and ecology (Crovello 1981; Kenkel et al. 1989). However, unlike most local ecological studies, the sampling unit is most often chosen after the data have been collected in regional biogeographical studies. Therefore, it is difficult to determine the potential influence of the size and shape of sampling unit on data collection and subsequent analyses and results. Both natural (e.g., watersheds) and arbitrary (e.g., latitude–longitude cells, equal-area quadrats) sampling units have been used in regional analyses (e.g., McAllister et al. 1986; Minns 1989). Watersheds and latitude–longitude cells vary in both size and shape. Such variation may confound the estimation of species richness for each sampling unit, and the results of the subsequent analyses. Square equal-area quadrats are not subject to these problems as quadrat size and shape are uniform. Therefore, square equal-area quadrats were used as the sampling unit in this study.

Species richness was determined for seven sizes of equal-area quadrats with sides measuring 15, 30, 60, 90, 120, 150, and 180 km. Quadrats with areas less than 25% in Ontario and in the poorly sampled Hudson Bay Lowlands (Mandrak and Crossman 1992*a*) were excluded from this study. To obtain precise estimates of species richness, the optimal quadrat size would be one for which between-quadrat variability is minimized (Kenkel et al. 1989). Mean number of species per quadrat, standard deviation, and coefficient of variation were measured for each quadrat size, and the quadrat size with the lowest coefficient of variation was used in further analyses.

Table 1. Mean, standard deviation, and range of the environmental and historical variables for eighty 90 × 90 km quadrats. Summary statistics for variables representing spatial heterogenity (except pH) are based on log-transformed data; summary statistics for all other variables are based on untransformed data. Note that log-transformed data (except pH) were used in all analyses.

Variable	Mean	SD	Range
Postglacial dispersal			
Minimum distance from dispersal corridor (km)	365.50	165.03	76.71–692.28
Mean distance from dispersal corridor (km)	764.84	154.95	550.04–1164.44
Spatial heterogeneity in distance from dispersal corridor (km)	5.66	0.49	4.42–6.32
Mean length of time covered by glacial lake (thousand years)	2.00	1.36	1.00–8.00
Spatial heterogeneity in length of time covered by glacial lake (thousand years)	0.46	0.42	0.00–1.58
Mean length of time since deglaciation (thousand years)	6.65	1.46	3.50–10.50
Spatial heterogeneity in time since deglaciation (thousand years)	0.32	0.27	0.00–1.10
Climate			
Growing degree-days	1266.09	235.36	818.11–1853.80
Spatial heterogeneity in growing degree-days	0.04	0.02	0.003–0.13
Mean monthly precipitation (mm)	67.76	8.12	51.83–88.68
Spatial heterogeneity in mean monthly precipitation (mm)	0.04	0.03	0.006–0.13
Annual variability in precipitation (mm)	22.54	4.82	13.03–31.59
Spatial heterogeneity in annual variability in precipitation (mm)	0.03	0.02	0.003–0.13
Mean annual temperature (°C)	3.42	2.32	0.71–8.72
Spatial heterogeneity in mean annual temperature (°C)	0.15	0.10	0.03–0.54
Annual variability in temperature (°C)	13.26	1.77	10.48–20.11
Spatial heterogeneity in annual variability in temperature (°C)	0.03	0.03	0.003–0.14
Elevation			
Elevation (m)	324.0	66.9	161.0–468.0
Spatial heterogeneity in elevation (m)	3.61	0.46	2.85–4.68
Lake Chemistry			
Mean annual alkalinity ($mg \cdot L^{-1}$ $CaCO_3$)	44.08	37.42	10.56–166.00
Spatial heterogeneity in mean annual alkalinity ($mg \cdot L^{-1}$ $CaCO_3$)	0.53	0.19	0.18–0.97
Annual variability in alkalinity ($mg \cdot L^{-1}$ $CaCO_3$)	1.32	0.25	1.05–2.30
Mean annual conductivity ($\mu mhos \cdot cm^{-1}$)	85.73	69.51	29.76–357.45
Spatial heterogeneity in mean annual conductivity ($\mu mhos \cdot cm^{-1}$)	0.46	0.15	0.10–0.80
Annual variability in conductivity ($\mu mhos \cdot cm^{-1}$)	1.29	0.22	1.06–2.24
Mean annual dissolved oxygen ($mg \cdot L^{-1}$)	9.54	0.39	8.14–10.52
Spatial heterogeneity in mean annual dissolved oxygen ($mg \cdot L^{-1}$)	0.12	0.05	0.03–0.36
Annual variability in dissolved oxygen ($mg \cdot L^{-1}$)	1.08	0.06	1.03–1.44
Mean annual pH	7.71	0.53	5.72–8.81
Spatial heterogeneity in mean annual pH	0.59	0.18	0.23–1.06
Annual variability in pH	0.29	0.17	0.07–1.07
Mean annual total dissolved solids (TDS) ($mg \cdot L^{-1}$)	62.32	48.41	22.64–241.29
Spatial heterogeneity in mean annual TDS ($mg \cdot L^{-1}$)	0.45	0.15	0.14–0.80
Annual variability in TDS ($mg \cdot L^{-1}$)	1.27	0.21	1.04–2.23
Lake morphometry			
Mean lake area (ha)	309.67	503.03	3.61–2913.16
Spatial heterogeneity in lake area (ha)	1.45	0.27	0.68–2.10
Mean maximum depth (m)	12.23	5.14	2.20–32.50
Spatial heterogeneity in maximum depth (m)	0.77	0.14	0.42–1.37
% summer stratification	64.72	22.47	11.20–97.60
Spatial heterogeneity in % summer stratification	0.42	0.07	0.15–0.52

Patterns of species richness

Spatial patterns in species richness were identified with the aid of mapping and spatial autocorrelation methods (e.g., Sokal 1979; Legendre and Fortin 1989). Moran's *I* coefficient was used to measure spatial autocorrelation in species richness. This coefficient is similar to Pearson's product-moment coefficient, and may have positive or negative values usually ranging between −1 and 1 (Legendre and Fortin 1989). The spatial structure of species richness was examined using correlograms where the values of Moran's *I* coefficient were plotted against the distance between quadrat centres. Characteristic shapes of the

correlograms are associated with specific spatial structures (Sokal 1979; Legendre and Fortin 1989). The spatial structure is termed isotropic if the spatial patterns are similar in different compass directions. If the spatial patterns differ in different directions, the spatial structure is termed anisotropic (Burrough 1987). To identify whether patterns of species richness are isotropic or anisotropic, an isotropic correlogram and directional correlograms (0° = north–south, 45° = northwest–southeast, 90° = east–west, 135° = southeast–northwest) were calculated using the GS+ software package (Gamma Design Software 1991).

Historical data

The historical data set was based on postglacial dispersal and contained seven variables (Table 1). All seven variables were log transformed ($\ln(x + 1)$) to standardize and normalize the distribution of the variables. Minimum, mean, and standard deviation values were calculated for the geographic distances (in kilometres) between the centres of each quadrat and the entry point of the five major postglacial dispersal routes into Ontario (Fig. 1) hypothesized by Mandrak and Crossman (1992*b*). Major dispersal routes were determined by comparing present-day species distributions to the locations of glacial waterbodies that acted as dispersal corridors (Mandrak and Crossman 1992*b*). The length of time that each quadrat has been deglaciated was determined by overlaying 372 regularly spaced points (Fig. 1) onto a series of maps depicting the location of the Wisconsinan ice sheet and glacial waterbodies in eastern North America between 18 000 and 5000 years ago at generally 1000-year intervals (Dyke and Prest 1987). The length of time that each quadrat was covered by glacial waterbodies was determined in the same manner. Two variables were created for each temporal measurement: a variable representing the mean value for each quadrat was determined by averaging the values at all points within the quadrat, and a variable representing the spatial heterogeneity within each quadrat was calculated as the standard deviation of the values at all points within the quadrat.

Environmental data

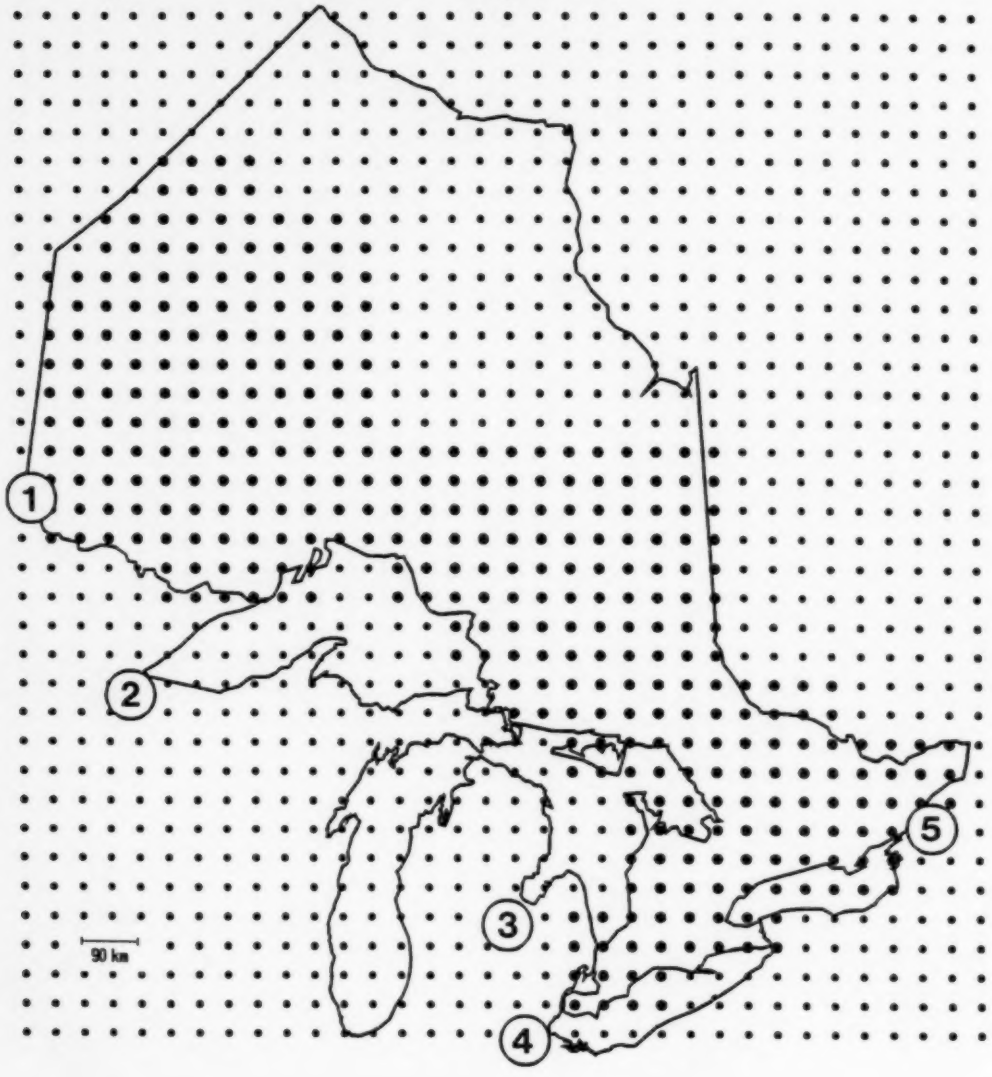
Four data sets of environmental measurements involved climate, elevation, lake chemistry, and lake morphometry (Table 1). All the environmental data, except pH, were log transformed ($\ln(x + 1)$) to standardize and normalize the distribution of the variables.

The climate data set contained 10 variables (Table 1). Climate data were obtained from the Digital Archive of Canadian Climatological Data (Atmospheric Environment Service of Environment Canada). These data represented total monthly precipitation and mean monthly temperature collected between 1960 and 1989 at 1836 recording stations (Fig. 2). Average values for total monthly precipitation and mean monthly temperature over the 30-year recording period were calculated for each station with a minimum sampling record of five consecutive years. Mean monthly precipitation and mean annual temperature at each station was calculated as the mean of the 12 monthly averages. Annual variability in temperature and precipitation at each station was calculated as the standard deviation of the 12 monthly averages. Growing degree-days were estimated for each station as $\sum$ [((mean monthly temperature > 5.5°C) − 5.5°C)30] (modified from Brown et al. 1980). To obtain data for areas of Ontario where climate recording stations were not present (Fig. 2), mean monthly precipitation, mean annual temperature, annual variability in precipitation and temperature, and growing degree-days were interpolated at 1224 regularly spaced points on a systematic sampling grid (Fig. 1) using the point (=punctual) kriging routine of the GS+ software package (Gamma Design Software 1991). Kriging is an optimal interpolation technique that uses a measure of the spatial variation (semivariance) in the actual data to estimate values at unsampled points. Estimation errors of the interpolated values indicate the reliability of these values (Burrough 1987). Three hundred and seventy-two of the 1224 regularly spaced interpolation points were within the study area (Fig. 1). Mean monthly precipitation, mean annual temperature, annual variability in precipitation and temperature, and growing degree-days were calculated for each quadrat as the mean of the interpolated values at all points within the quadrat. The spatial heterogeneity of these five variables within each quadrat was calculated using the standard deviation of the interpolated values at all points within the quadrat.

The elevation data set contained two variables, mean elevation and an estimate of spatial heterogeneity in elevation (Table 1). Elevation was obtained for 11 137 sites from raw data in the OMNR Lake Inventory data base (9886 stations), the Digital Archive of Canadian Climatological Data (1836 stations), and an unpublished Algonquin Park data base (995 stations). Mean elevation was calculated for each quadrat as the mean of the elevation values of all sites within the quadrat. The spatial heterogeneity of elevation within each quadrat was calculated as the standard deviation of the elevation values of all sites within the quadrat.

Lake chemistry and morphometry data for 9886 lakes were obtained from the OMNR Lake Inventory data base (for methodology see Dodge et al. 1985). The lake chemistry data set contained 15 variables (Table 1). These data represented surface (depth ≤2.0 m) measurements for pH, alkalinity (milligrams of $CaCO_3$ per litre), specific conductivity (micromhos per centimetre), dissolved O_2 (milligrams per litre), and total dissolved solids (milligrams per litre). For most lakes in the OMNR Lake Inventory, these measurements were taken on a single date. Therefore, temporal trends in these data cannot be examined in individual lakes, but trends may be determined within quadrats. For each lake, the data were partitioned by month of record. For each of the five measurements, average monthly values were calculated as the average of the values for all lakes within each quadrat by month. Mean annual variables for each of the five measurements were calculated for each quadrat as the mean of the average monthly values. Annual variability for each of the five measurements were calculated for each quadrat as the standard deviation of the average monthly values. The spatial heterogeneity of the five mean annual variables within each quadrat was

Fig. 1. Points on a systematic sampling grid used to interpolate values for climate variables. Large dots represent points used to determine values for each quadrat. Small dots represent points used in the kriging analysis, but not present in a quadrat. Circled numbers indicate entry location of postglacial dispersal routes (from Mandrak and Crossman 1992*b*): 1 = Glacial Lake Agassiz; 2 = Brule-Portage Outlet; 3 = Grand Valley Outlet; 4 = Fort Wayne Outlet; 5 = Champlain Outlet.



calculated as the mean of the standard deviation for each of the 12 monthly averages within the quadrat. Any quadrats that contained fewer than 10 lakes with lake chemistry data were excluded from further analyses.

The lake morphometry data set contained six variables representing lake area, maximum depth, and summer stratification (Table 1). Mean lake area and mean maximum depth were calculated for each quadrat using all lakes within the quadrat. The spatial heterogeneity of lake area and maximum depth within each quadrat were calculated as the standard deviation of lake area and maximum depth for all lakes within the quadrat. The percentage of lakes in each quadrat that exhibit summer stratification was estimated as a function of thermocline depth and maximum depth. Thermocline depth was predicted using the equation: $\ln(\text{thermocline depth}) = 0.185\ln(\text{lake area}) + 0.842$ (Hanna 1990). If the predicted thermocline depth was greater than maximum depth, it was assumed that the lake did not stratify. The spatial heterogeneity of summer stratification within each quadrat was calculated as the standard

Fig. 2. Distribution of climate recording stations in the Digital Archive of Canadian Climatological Data for the period of 1960–1989.

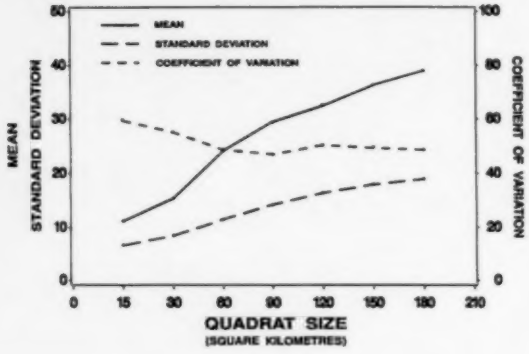
deviation of the presence or absence of stratification (i.e., 1 = stratification; 0 = no stratification) for all lakes within the quadrat.

Modelling relationships among species richness, historical and environmental data, and geographic distance

Relationships among species richness, the historical and environmental data sets, and geographic distances were investigated using the Mantel test (Mantel 1967). This test measures the correlation between two matrices and assesses the significance of the correlation by normal approximation, or by randomizing one of the matrices and calculating a null distribution of values from the randomly generated associations (Jackson and Somers 1989; Legendre and Fortin 1989). In this study, the Mantel test was calculated using the NTSYS-pc software package (Rohlf 1992), and 1000 random matrix permutations were used to assess significance levels. Triangular Euclidean distance matrices were calculated for the richness data and each historical and environmental data set. Nonsignificant correlations between the richness and historical or environmental matrices indicated relationships were not detectable between the data sets. Significant correlations may indicate causal relationships or spurious relationships as the result of the confounding effect of spatial autocorrelation or some other variable(s) that were not measured.

To test for the presence of spatial autocorrelation, a triangular geographic distance matrix was created by measuring the distances (in kilometres) between all possible

Fig. 3. Mean (solid line), standard deviation (dotted line) and coefficient of variation (broken line) of species richness for seven sizes of quadrats.



pairs of quadrats. If the correlations between the Euclidean distance matrices and the geographic distance matrices were not significant and positive, the data were assumed not to be spatially autocorrelated. Significant, positive correlations between the Euclidean distance matrices and geographic distance matrix indicated distant quadrats exhibit regional spatial autocorrelation (Legendre and Fortin 1989).

Spatial autocorrelation was partialled out of the richness, historical, and environmental matrices using the partial Mantel test of Smouse et al. (1986). This method performed most reliably relative to several other partial correlation techniques used in matrix comparisons (Oden and Sokal 1992). The off-diagonal elements of each Euclidean distance matrix were separately regressed against the off-diagonal elements of the geographic distance matrix. The resultant residual matrix (hereafter, termed the spatially corrected matrix) for each historical and environmental data set was compared with the spatially corrected matrix for the richness data using the Mantel test. If the correlations were nonsignificant, it was concluded that no relationships exist and any significant uncorrected correlations were the result of a common spatial structure. Significant correlations may indicate causal relationships.

The historical and environmental Euclidean distance matrices were separately subjected to principal coordinates analysis (PCoA) to provide a summary of the dominant trends in each matrix, and thereby identify particular variables within each matrix that are strongly related to the richness data. For each data set, the loadings of each variable on the first three principal coordinate axes were determined using Pearson's product-moment correlation. The results of the PCoA were reported only for the spatially corrected historical and environmental matrices significantly correlated to the spatially corrected richness matrix.

In summary, the significance of the relationships between species richness and each historical and environmental data set was assessed using the Mantel test and partial Mantel test, and the importance of particular variables within each of the historical and environmental matrices significantly related to richness was identified with the aid of PCoA.

Results

Patterns of species richness

The optimal quadrat size was determined to be 90 × 90 km. At this size, the coefficient of variation is minimum (Fig. 3). Eighty 90-km quadrats, containing richness data and sufficient environmental data, were used in subsequent analyses. Richness ranged from 59 species per quadrat in southwestern Ontario to 17 species per quadrat in northern Ontario (Fig. 4). Variation in the shapes of the correlograms based on richness (Fig. 5) indicated the spatial structure of species richness was not isotropic. The overall correlogram showed that neighbouring quadrats (within three distance classes [=270 km] of each other) exhibited positive autocorrelation, and distant quadrats (greater than 450 km from each other) exhibited negative autocorrelation. The overall correlogram appeared to represent a composite of the directional correlograms. In the north–south (N–S) correlogram, neighbouring quadrats were positively correlated, and more distant quadrats were negatively correlated, revealing a steep linear gradient. This pattern represented the strong low–high, N–S richness gradient evident in Fig. 4. The northeast–southwest (NE–SW) correlogram exhibited a short gradient that represented a low–high, NE–SW richness gradient truncated in the northeast by the Hudson Bay Lowlands and Quebec border; and, to the southwest by the Great Lakes in southern Ontario, and the Manitoba and Minnesota borders in northern Ontario (Fig. 4). The east–west (E–W) correlogram indicated that both neighbouring and distant quadrats are positively correlated, while quadrats at intermediate distances are uncorrelated. This pattern reflected a high–low–high, E–W richness gradient (Fig. 4). In the northwest–southeast (NW–SE) correlogram, neighbouring quadrats were positively correlated, quadrats at intermediate distances were uncorrelated, and distant quadrats were negatively correlated. This pattern represented a low–high, NW–SE richness gradient (Fig. 4).

The Euclidean distance matrix based on fish species richness was significantly and positively correlated to the geographic distance matrix (Mantel $Z = 0.45$, $p \leq 0.001$). Therefore, the Mantel test corroborated that richness exhibited an overall regional spatial autocorrelation as indicated by the correlograms (Fig. 4).

Relationships among species richness, historical and environmental data, and geographic distance

The richness Euclidean distance matrix was significantly correlated to each historical and environmental Euclidean distance matrix except elevation (Table 2). The significant, positive correlation between each Euclidean distance matrix and geographic distance matrix indicated that each matrix exhibits regional spatial autocorrelation (Table 2). After the effect of regional spatial autocorrelation was partialled out, only the Mantel correlations between richness and climate, and postglacial dispersal, were significant (Table 2).

Eighty-eight percent of the variation in the postglacial dispersal data was summarized by the first three PCoA axes (Table 3). The first axis (47.2%) contrasted length of time of deglaciation and coverage by glacial lakes, with

Fig. 4. Fish species richness in Ontario lakes based on 90 × 90 km equal-area quadrats.

distance from dispersal corridors. The second (32.2%) and third (8.9%) axes represented gradients associated with glacial lake coverage. A plot of the first two PCoA axes contrasted northeastern quadrats distant from dispersal corridors with quadrats around the Great Lakes that have been deglaciated and covered by glacial lakes for the greatest length of time (Fig. 6).

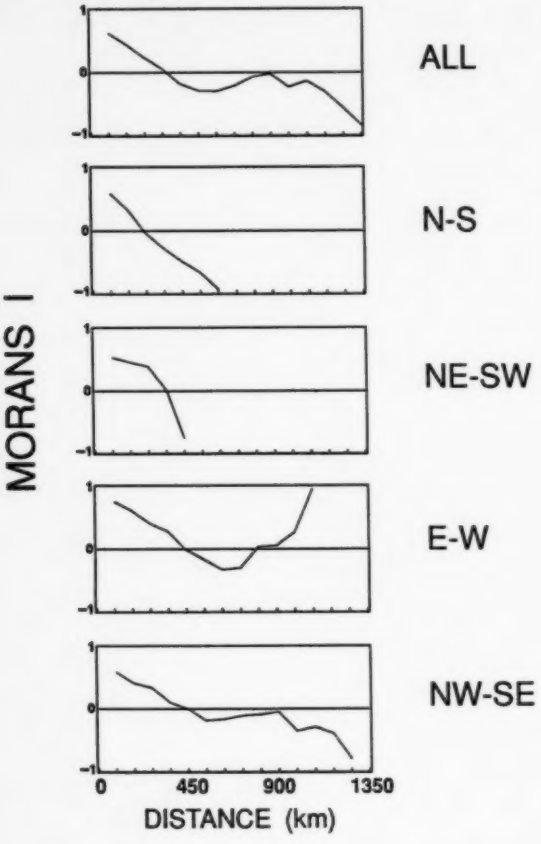
Ninety-six percent of the variation in the climate data was summarized by the first three PCoA axes (Table 3). The first axis accounted for most of the variation (85.7%) and represented a predominant temperature-related gradient and a precipitation-related gradient. The second axis (7.7%) contrasted mean annual precipitation with annual variability in precipitation and temperature. The third axis (2.9%) represented a growing degree-days gradient. A plot of the first two PCoA axes contrasted southern quadrats containing a warm, wet climate with locally variable precipitation and seasonally variable temperature with more northern quadrats that exhibit a cool, dry climate with seasonally variable precipitation (Fig. 7).

Discussion

Patterns of fish species richness are anisotropic in Ontario. The simple, steep, linear gradients present in the N–S and NE–SW orientations are consistent with a latitudinal gradient often reported in richness studies (e.g., McAllister et al. 1986; Matuszek and Beggs 1988). Barbour and Brown (1974) suggested latitudinal gradients may reflect gradients related to factors such as postglacial dispersal and climate. Minns (1989) identified species distribution patterns in Ontario as changing from southwest to northeast, and hypothesized these patterns to be the result of some regional effects, not examined in his study, such as postglacial dispersal and climate. In this study, postglacial dispersal and climate were significantly correlated with species richness after the effects of spatial autocorrelation were partialled out.

The species richness of any area is, in part, a function of the size of the species pool, primarily dependent upon historical processes (Tonn 1990), available to colonize the area. In recently deglaciated areas such as Ontario, regional

Fig. 5. Correlograms of fish species richness in Ontario: overall correlogram (ALL); directional correlograms representing north–south (N–S), northeast–southwest (NE–SW), east–west (E–W), and northwest–southeast gradients (NW–SE). Moran's *I* coefficient is based on a minimum of 10 centroid pairs.



species pools were determined by the extent and chronology of glacial lakes and outlets that acted as dispersal corridors (Radforth 1944; Mandrak and Crossman 1992*b*) and by the vagility and thermal tolerance of the species that utilized these corridors. In this study, greater species richness is found in quadrats that were close to the entry location of dispersal corridors into Ontario and were deglaciated and covered by glacial lakes for the longest periods of time (Fig. 7). The highest lake species richness is found in quadrats in southern Ontario and northwestern Ontario (Fig. 4). Quadrats in southern Ontario were covered for long periods of time by glacial lakes in the Great Lakes basin and were close to the Fort Wayne, Grand Valley, Mohawk, and Champlain dispersal corridors (Fig. 1; Mandrak and Crossman 1992*b*). Quadrats in northwestern Ontario were covered for long periods of time by glacial Lake Agassiz, which acted as a dispersal corridor, and were close to the Brule-Portage dispersal corridor (Fig. 1; Mandrak and Crossman 1992*b*). Glacial Lake Agassiz and the Brule-Portage, Fort Wayne, Grand Valley, and Warren outlets acted as dispersal corridors for species originating in the Mississippian refugium, which contributed the highest number of species to the Ontario fish fauna. Compared with other glacial refugia, the Mississippian refugium had the largest species pool and the earliest, longest, and most numerous postglacial aquatic connections to Ontario (Mandrak and Crossman 1992*b*). Although it had a smaller species pool, the Atlantic Coastal refugium contributed species not found in other glacial refugia to southern Ontario, thus enhancing species richness (Mandrak and Crossman 1992*b*).

Greater species richness is associated with quadrats containing warm, wet climates with locally variable precipitation and seasonally variable temperature (Fig. 7). Temperate zone climates exhibit a seasonality that results in an annual cycle of resource abundance and resource scarcity for the biota (Shuter and Post 1990). The period of resource abundance shortens and the period of scarcity lengthens in more northern temperate and subarctic areas. The northern limit of the range of any species occurs at the point where the short growing season and long period of resource scarcity will not allow a viable population to be maintained (Shuter and Post 1990). The northern range limits of individual species have been modelled using mean annual air temperature (e.g., Shuter et al. 1980; Johnson and Evans 1990; Shuter and Post 1990). Mean annual air temperature is the dominant variable in the PCoA based on the climate matrix (Table 3); therefore, the physiological requirements for growth of individual fish species (as estimated by temperature) are likely important in structuring patterns of species richness. As temperature decreases in northern and northeastern quadrats, the minimum growth in young-of-the-year required to maintain a viable population is probably not met by many species. This would lead to high overwinter mortality of young-of-the-year, and the eventual extirpation of these species (Oliver et al. 1979; Shuter et al. 1980; Shuter and Post 1990). Other important variables such as precipitation and growing degree-days may reflect productivity (Richerson and Lum 1980). These variables exhibit similar patterns to temperature; thus, productivity would be greatest in southern quadrats and decrease towards northern and northeastern quadrats. Higher primary productivity may increase the number of coexisting species, as greater energy flow may be partitioned among a greater number of species to sustain a minimum viable population (Hutchinson 1959; Connell and Orias 1964; Currie 1991). A corollary to this concept is that climatic stability (i.e., climate with little annual variability) would permit a more constant influx of resources, which would allow a finer degree of resource exploitation and greater niche separation (Richerson and Lum 1980; Owen 1989). However, in this study, a greater climatic stability is present in the northern quadrats, but these quadrats contain fewer species than the southern quadrats. It appears that "climatic favourableness" (Whittaker 1972; estimated as mean annual air temperature by Richerson and Lum (1980)) is more important in structuring richness in north temperate and subarctic zones where resources are limited. In Ontario, climatic favourableness would be highest in southern quadrats. These quadrats would have longer periods of resource abundance which would lead

Table 2. Results of Mantel tests between the richness Euclidean distance matrix, environmental Euclidean distance matrices, and geographic distance matrix. Values above the diagonal represent Mantel correlations, and values below the diagonal represent partial Mantel correlations after geographic distance is partialled out. Significance levels based on 1000 permutations: * = $p \leq 0.01$; ** = $p \leq 0.001$.

	1	2	3	4	5	6
Geographic distance	0.37**	0.30**	0.48**	0.28**	0.23**	0.64**
1. Richness	—	0.44**	0.46**	0.05	0.13*	0.19**
2. Postglacial dispersal	0.32**	—	0.44**	0.24**	0.20**	0.08
3. Climate	0.36**	0.35**	—	0.29**	0.31**	0.28**
4. Elevation	0.02	0.18*	0.19**	—	0.31**	0.11
5. Lake chemistry	0.06	0.14*	0.23**	0.26**	—	0.39**
6. Lake morphometry	−0.01	−0.16*	−0.04	−0.07	0.32**	—

Table 3. Bivariate correlations between postglacial dispersal and climate variables, and the principal coordinate scores based on the Euclidean distance matrices.

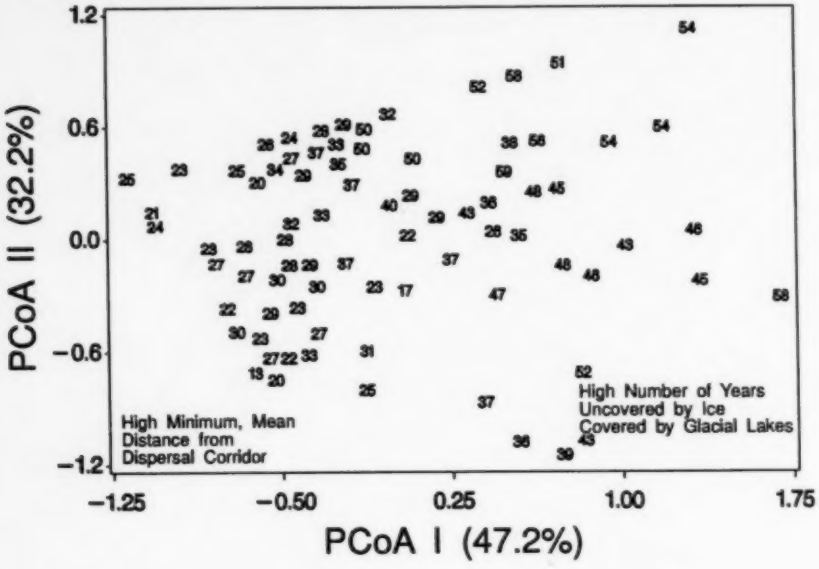
	PCo1	PCo2	PCo3
Postglacial dispersal (% variation explained)	47.2	32.2	8.9
Correlations			
Minimum distance from dispersal corridor	−0.97	−0.24	0.03
Mean distance from dispersal corridor	−0.63	−0.18	−0.34
Spatial heterogeneity in distance from dispersal corridor	0.03	−0.34	−0.13
Mean length of time covered by glacial lake	0.39	−0.91	−0.14
Spatial heterogeneity in length of time covered by glacial lake	0.27	−0.56	0.74
Mean length of time since deglaciation	0.85	0.10	0.09
Spatial heterogeneity in time since deglaciation	−0.17	−0.10	−0.004
Climate (% variation explained)	85.7	7.7	2.9
Correlations			
Growing degree-days	−0.72	0.19	0.66
Spatial heterogeneity in growing degree-days	−0.32	0.13	−0.36
Mean monthly precipitation	−0.52	0.67	0.00
Spatial heterogeneity in mean monthly precipitation	−0.55	0.24	−0.10
Annual variability in precipitation	0.61	−0.73	0.14
Spatial heterogeneity in annual variability in precipitation	−0.61	0.46	0.07
Mean annual temperature	−0.99	−0.08	−0.03
Spatial heterogeneity in mean annual temperature	0.18	0.39	−0.24
Annual variability in temperature	0.61	−0.55	−0.10
Spatial heterogeneity in annual variability in temperature	0.04	−0.08	−0.31

to increased growth, higher overwinter survival of young-of-the-year, and the maintenance of viable populations for many fish species. In northern quadrats, where climatic stability is highest, climatic favourableness is low. Northern quadrats exhibit little annual variability in long periods of resource scarcity, which results in many species failing to maintain viable populations.

The relationships between the fish species richness and elevation, lake chemistry, and lake morphometry matrices were not significant after spatial autocorrelation was partialled out. This suggests that the presence of spatial autocorrelation resulted in type I error: failing to accept the null hypothesis (i.e., there is no significant difference between the richness and elevation, lake chemistry, or lake morphometry data matrices).

Elevation has been used in richness studies as a surrogate variable for habitat heterogeneity (e.g., Richerson and Lum 1980; Owen 1989; Currie 1991) and historical factors such as postglacial dispersal and isolation (e.g., Matuszek and Beggs 1988; Minns 1989). Significant correlations existed between the elevation matrix and the postglacial dispersal and climate matrices when spatial autocorrelation was partialled out (Table 2), but the relationship between elevation and postglacial dispersal was only weakly significant. Areas of higher elevation were more likely to be deglaciated for longer periods allowing more time for colonization by species but were less likely to be covered by glacial lakes resulting in reduced access for colonization. Consequently, elevation may act only in part as a surrogate for postglacial dispersal. The significant relationship

Fig. 6. Plot of the first and second PCoA axes based on the postglacial dispersal data. Numbers represent species richness as recorded in Fig. 4.



between elevation and climate is not suprising as such relationships are well-known phenomena (Brown et al. 1980). A significant correlation also existed between the elevation matrix and lake chemistry matrix after geographic distance was partialled out (Table 2). Because the first PCoA axis based on the elevation matrix accounted for over 82% of the variation in the data set and represented spatial heterogeneity in elevation, elevation may, in part, also act as a surrogate for lake chemistry heterogeneity.

Lake chemistry (particularly pH) and lake morphometry (particularly area) have been hypothesized to structure richness patterns as measures of productivity (e.g., Minns 1989), habitat heterogeneity (e.g., Barbour and Brown 1974; Eadie and Keast 1984; Eadie et al. 1986; Minns 1989), or as limiting factors (e.g., Matuszek and Beggs 1988; Matuszek et al. 1990; Shuter and Post 1990). In several of these studies (e.g., Barbour and Brown 1974; Eadie et al. 1986; Matuszek and Beggs 1988), significant correlations were present between richness and morphometry and chemistry variables as well as between richness and latitude, which may indicate that spatial autocorrelation was present in these data. The influence of latitude or spatial autocorrelation was not investigated in the other studies. The results of the present study indicated lake chemistry and lake morphometry exhibit significant spatial autocorrelation, and were significantly related to richness. However, these data were not related to richness after the effects of spatial autocorrelation were removed. Therefore, the conclusions of the earlier studies may reflect type I error. The first PCoA axis based on the lake morphometry matrix, which exhibited the greatest spatial autocorrelation (Table 2), accounted for close to 88% of the variation in the data set and represented a lake area gradient ($r = -0.99$). These observations indicate the use of species richness – area equations derived from regional data to estimate local richness or the number of species lost as the result of acidification will lead to erroneous conclusions unless the effects of spatial autocorrelation were controlled in developing the original equation.

Minns (1989) and Jackson and Harvey (1989) suggested that local factors, such as lake morphometry and pH, were dominant in explaining species richness in Ontario lakes and hypothesized that regional community structure was dependent on postglacial dispersal and climate but independent of lake morphometry and pH. The results of this study suggest that postglacial dispersal and climatic processes structure regional patterns of fish species richness in Ontario lakes; whereas, elevation, lake chemistry, and lake morphometry do not influence lake species richness at the scale of this study. These factors may influence local patterns of fish species richness, but such relationships must be examined after removing the effects of spatial autocorrelation.

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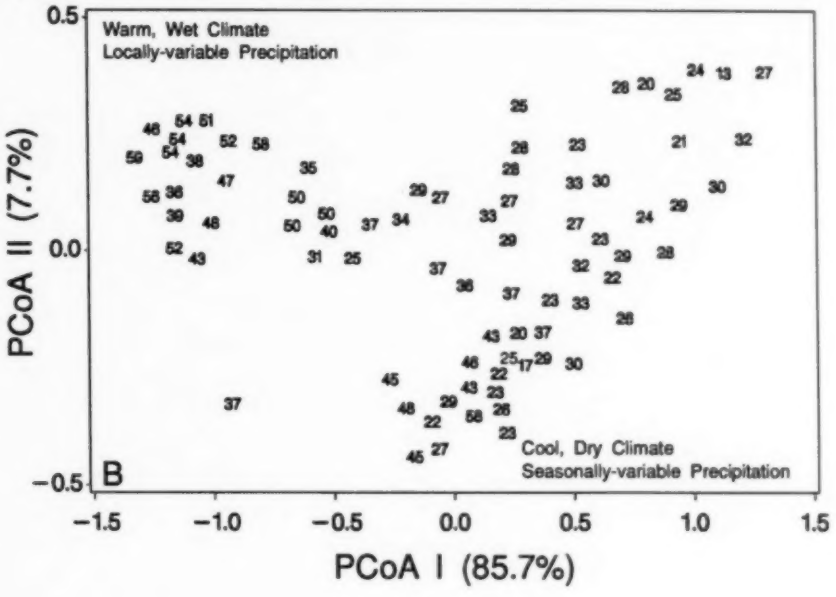
Fig. 7. Plot of the first and second PCoA axes based on the climate data. Numbers represent species richness as recorded in Fig. 4.



References

Barbour, C.D., and J.H. Brown. 1974. Fish species diversity in lakes. Am. Nat. 108: 473–489.

Bivand, R. 1980. A Monte Carlo study of correlation coefficient estimation with spatially autocorrelated observations. Quaest. Geogr. 6: 5–10.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology, 73: 1045–1055.

Bowlby, J.N., and D. Green. 1987. Efficiency of aquatic habitat inventory surveys in the assessment of fish species present. Ont. Min. Nat. Res. Fish. Acid. Rep. Ser. 87-08: 39 p.

Brown, D.M., G.A. McKay, and L.J. Chapman. 1980. The climate of southern Ontario. Atmospheric Environment Service, Environment Canada, Ottawa, Ont. Climatol. Stud. 5: 67p.

Burrough, P.A. 1987. Spatial aspects of ecological data, p. 213–251. *In* R.H.G. Jongman, C.J.F. ter Braak, and O.F.R. van Tongerrn [ed.] Data analysis in community and landscape ecology. PUDOC Wageningen, The Netherlands.

Connell, J.H., and E. Orias. 1964. The ecological regulation of species diversity. Am. Nat. 113: 791-833.

Crovello, T.J. 1981. Quantitative biogeography: an overview. Taxon, 30: 563–575.

Currie, D.J. 1991. Energy and broad-scale patterns of animal- and plant-species richness. Am. Nat. 137: 27–49.

Dodge, D.P., G.A. Goodchild, J.C. Tilt, and D.G. Waldriff. 1985. Manual of instructions: aquatic habitat inventory surveys. Fisheries Policy Branch, Ontario Ministry of Natural Resources, Toronto, Ont. 167 p.

Dyke, A.S., and V.K. Prest. 1987. Paleogeography of northern North America 18,000–5,000 years ago. Geological Survey of Canada, Ottawa, Ont. Map 1703A.

Eadie, J.M., and A. Keast. 1984. Resource heterogeneity and fish species diversity in lakes. Can. J. Zool. 62: 1689–1695.

Eadie, J.M., T. Andrew-Hurly, R.D. Montgomerie, and K.L. Teather. 1986. Lakes and rivers as islands: species–area relationships in the fish faunas of Ontario. Environ. Biol. Fishes, 15: 81–89.

Gamma Design Software. 1991. GS+: geostatistics for the agronomic and biological sciences, version 1.1 edition. Gamma Design Incorporated, Plainwell, Mich.

Hanna, M. 1990. Evaluation of models predicting mixing depth. Can. J. Fish. Aquat. Sci. 47: 940–947.

Harvey, H.H. 1978. Fish communities of the Manitoulin Island lakes. Verh. Int. Ver. Theor. Angew. Limnol. 20: 2031–2038.

Harvey, H.H. 1981. Fish communities of the lakes of the Bruce Peninsula. Verh. Int. Ver. Theor. Angew. Limnol. 21: 1222–1230.

Hinch, S.G. 1991. Small- and large-scale studies in fisheries ecology: the need for cooperation among the researchers. Fisheries (Bethesda), 16(3): 22–27.

Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Am. Nat. 93: 145–159.

Jackson, D.A., and H.H. Harvey. 1989. Biogeographic associations in fish assemblages: local versus regional processes. Ecology, 70: 1472–1484.

Jackson, D.A., and K.M. Somers. 1989. Are probability estimates from the permutation model of Mantel's test stable? Can. J. Zool. 67: 766–769.

Johnson, T.B., and D.O. Evans. 1990. Size-dependent winter mortality of young-of-the-year white perch: climate warming and invasion of the Laurentian Great Lakes. Trans. Am. Fish. Soc. 119: 301–313.

Kenkel, N.C., P. Juhasz-Nagy, and J. Podani. 1989. On sampling procedures in population and community ecology. Vegetatio, 83: 195–207.

Legendre, P. 1990. Quantitative methods and biogeographic analysis, p. 9–34. *In* D.J. Garbary and R.R. South [ed.]

Evolutionary biogeography of the marine algae of the North Atlantic. NATO ASI Ser. G22.
Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology, 74: 1659–1673.
Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio, 80: 107–138.
Legendre, P. and M. Troussellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. Limnol. Oceanogr. 33: 1055–1067.
Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology, 73: 1943–1967.
Mandrak, N.E., and E.J. Crossman. 1992*a*. A checklist of Ontario freshwater fishes annotated with distribution maps. R. Ont. Mus. Life Sci. Publ. 186 p.
Mandrak, N.E., and E.J. Crossman. 1992*b*. Postglacial dispersal of freshwater fishes into Ontario. Can. J. Zool. 70: 2247–2259.
Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27: 209–220.
Matuszek, J.E., and G.L. Beggs. 1988. Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. Can. J. Fish. Aquat. Sci. 45: 1931–1941.
Matuszek, J.E., J. Goodier, and D.L. Wales. 1990. The occurrence of Cyprinidae and other small fish species in relation to pH in Ontario lakes. Trans. Am. Fish. Soc. 119: 850–861.
McAllister, D.E., S.P. Platania, F.W. Schueler, M.E. Baldwin, and D.S. Lee. 1986. Ichthyofaunal patterns on a geographic grid, p. 18–51. *In* C.H. Hocutt and E.O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, N.Y.
Minns, C.K. 1986. A model of bias in lake selection for survey. Can. Tech. Rep. Fish. Aquat. Sci. 1496: 21 p.
Minns, C.K. 1989. Factors affecting fish species richness in Ontario lakes. Trans. Am. Fish. Soc. 118: 533–545.
Oden, N.L., and R.R. Sokal. 1992. An investigation of three-matrix permutation tests. J. Classif. 9: 275–290.
Oliver, J.D., G.F. Holeton, and K.E. Chua. 1979. Overwintering mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Trans. Am. Fish. Soc. 108: 130–136.
Owen, J.G. 1989. Patterns of herpetofaunal species richness: relation to temperature, precipitation, and variance in elevation. J. Biogeogr. 16: 141–150.
Radforth, I. 1944. Some considerations on the distribution of fishes in Ontario. Contrib. R. Ont. Mus. Zool. 25: 116 p.
Richerson, P.J., and K.L. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. Am. Nat. 116: 504–536.
Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. Science (Washington, D.C.), 235: 167–171.
Rohlf, F.J. 1992. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 1.70 edition. Applied Biostatistics Incorporated, Setauket, N.Y.
Shuter, B.J. and J.R. Post. 1990. Climate, population variability, and the zoogeography of temperate fishes. Trans. Am. Fish. Soc. 119: 314–336.
Shuter, B.J., J.A. MacLean, F.E.J. Fry, and H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. Fish. Soc. 109: 1–34.
Smouse, P.E., J.C. Long, and R.R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel Test of Matrix Correspondence. Syst. Zool. 35: 627–632.
Sokal, R.R. 1979. Testing statistical significance of geographic variation patterns. Syst. Zool. 28: 227–231.
Somers, K.M., and H.H. Harvey. 1984. Alteration of fish communities in lakes stressed by acid deposition and heavy metals near Wawa, Ontario. Can. J. Fish. Aquat. Sci. 41: 20–29.
Tonn, W.M. 1990. Climate change and fish communities: a conceptual approach. Trans. Am. Fish. Soc. 119: 337–352.
Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, 21: 213–251.

Variations in the contribution of transport to changes in planktonic animal abundance: a study of the flux of fish larvae in Conception Bay, Newfoundland[1]

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Abstract: We investigated the magnitude of short-term variations in the flux of several species of fish larvae in Conception Bay, Newfoundland, determined the contribution of these fluxes to changes in the abundance of these species, and assessed the factors that may be causing the variations in these fluxes. The net effect of transport ranged from a daily influx of 5.8% to a daily efflux of 6.2% from the population. Short-term variations in transport were associated with variations in wind stress. The contribution of transport to variations in population abundance ranged from 12 to more than 75% of the average daily rate of change in numbers for the different species. The contribution of physical processes to estimated mortality rates is variable and can have a significant impact on the investigation and interpretation of potential biological processes (e.g., predation and starvation) influencing the survival of larval fish. We predicted that the average correction to the instantaneous mortality rate due to advection and diffusion should be proportional to $A^{-1/2}$, where A is the area of system under study. This highlights the susceptibility of small systems to estimation error of mortality rates caused by short-term variations in physical forcing.

Résumé : Nous avons examiné l'ampleur des variations à court terme dans le flux des larves de plusieurs espèces de poissons dans la baie Conception (Terre-Neuve), mesuré la contribution de ces flux aux changements d'abondance de ces espèces et évalué les facteurs qui peuvent causer ces variations. L'effet net du transport allait d'un apport quotidien de 5,8% à une exportation quotidienne de 6,2% de la population. Les variations à court terme du transport étaient associées à des variations de la force du vent. La contribution du transport aux variations d'abondance de la population allait de 12 à plus de 75% du taux quotidien moyen de modification de l'effectif des différentes espèces. La contribution des processus physiques aux taux de mortalité estimés est variable et peut avoir un effet significatif sur l'étude et l'interprétation des processus biologiques potentiels (p. ex. prédation en inanition) qui influencent la survie des larves de poissons. Nous avons prédit que la correction moyenne du taux instantané de mortalité due à l'advection et à la diffusion devrait être proportionnelle à $A^{-1/2}$, A étant la superficie du système à l'étude. Cela met en lumière la vulnérabilité des petits systèmes aux erreurs d'estimation du taux de mortalité causées par les variations à court terme du forçage physique.
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Introduction

Harden Jones' (1968) model of migrations through the life history of fishes proposes that the egg and larval stages drift passively with ocean currents. Iles and Sinclair (1982) and Sinclair (1988) present an alternative theory in which a population's integrity and reproductive success relies on retention of eggs and larvae within a specific hydrographic regime. A common feature of both these frameworks is the relationship of the early life stages of fish to the physical oceanographic characteristics of their environment. In

both these hypotheses, the significance of this relationship in determining the retention or loss of fish eggs and larvae from a population is of utmost importance (Bakun and Parrish 1982; Sinclair 1988). Transport can directly affect changes in animal abundance in a study area through immigration or emigration, and indirectly by moving animals into regions of differing suitability for survival.

Fluctuations in abundance of larval fish are often interpreted as mortality and are often attributed to predation or starvation. However, understanding the relationship between egg and larval dispersal and circulation regimes is essential in avoiding misconceptions about the significance of trophic interactions (e.g., predation, feeding) in determining survival (Taggart and Frank 1990). The relative significance of transport to variations in larval fish abundance may be greatly influenced by the relative size of the system and by the nature of the physical environment itself. Although physical losses may be relatively unimportant in quiescent seas or on large banks (e.g., Kim and Bang 1990; Frank et al. 1992), their importance may be substantial in smaller systems such as rivers, estuaries, and small bays (e.g., Taggart and Leggett 1987) or in upwelling systems (Bailey 1981; Hewitt and Methot 1982; Shelton and Hutchings 1982; Power 1986). Furthermore, the relative contribution of advection and diffusion to the apparent variations in abundance may fluctuate over time because of variations in environmental driving forces (e.g., winds).

Most studies of larval mortality that account for the physical fluxes of fish eggs and (or) larvae have been Lagrangian or semi-Lagrangian based: patches of eggs and (or) larvae are tracked and changes in abundance are estimated in space and time. Sometimes populations are monitored on a fixed grid as the patch drifts through the study area (McGurk 1989; Kim and Bang 1990). More often a patch is tagged with one or more drifting buoys, and egg and (or) larval densities are monitored over the estimated patch area (Talbot 1977; Fortier and Leggett 1985; Munk et al. 1986; Heath and MacLachlan 1987; Reed et al. 1989). Abundances are estimated either by integrating density over the full patch, or by adjusting the measured density to account for the imperfectly known increase in patch area resulting from differential advection (shear dispersion) and diffusion. In most cases it is necessary, somewhat arbitrarily, to define a patch boundary. The imperative in Lagrangian based experiments is to sample over a large enough region to define the patch and to adequately sample the low larval densities near the patch boundary. To confound matters, the effects of advection and diffusion on abundance is often estimated solely from changes in population density. Consequently, parameter estimates for biological and physical losses are inevitably correlated and severely hamper the understanding of the factors contributing to changes in abundance.

By contrast, an experiment limited to a semienclosed area like Conception Bay adopts an Eulerian frame: a fixed grid is used to estimate the total number of larvae within the bay, and the problem of patch dispersion does not appear because the area is fixed (Taggart and Leggett 1987). The experimental imperative shifts to that of obtaining an accurate larval census as well as estimating the flux across the open boundary. Both changes in abundances and the fluxes are estimated independently, which allows a less restricted interpretation of the observations.

In this paper, we report the results of an Eulerian study larval fish fluxes from Conception Bay (47°45′N, 53°00′W), Newfoundland (Fig. 1). Our objectives were to (1) determine the magnitude and short-term variations in the fluxes of larvae; (2) determine the contribution of these fluxes to the changes in abundance of larvae in the bay; and (3) assess the factors that may cause variations in these fluxes. Finally, we contrast our results with previous studies to assess possible scale dependency. Conception Bay is an area just small enough to permit the frequent surveys essential to the study of environmental conditions and organisms that undergo rapid changes in dynamics or abundance. Variations in the exchange of mass with the open ocean are also readily monitored. Finally, Conception Bay is a spawning area for several species of fish (Frank and Leggett 1982; Laprise and Pepin 1995), which allows us to compare the dynamics of several species and to evaluate the potential significance of transport on variations in abundance. In contrast to other studies that compare the response of a single species in one system with results from studies of other systems and species, which can differ in approach and reliability, our investigation of Conception Bay provides the opportunity to assess whether there are significant differences among species of larvae exposed to the same environmental factors.

Materials and methods

Study site

Conception Bay is approximately 50 km long and 25 km wide with a maximum depth exceeding 300 m and a total surface area of about 1000 km^2 (Fig. 1). A 150-m sill at the mouth separates the bay from the slightly shallower northern Grand Bank. Mean currents are weak and display no coherent spatial pattern. Tides are also meagre with currents ≤ 0.02 $m \cdot s^{-1}$ (B. deYoung, Memorial University of Newfoundland, St. John's, Nfld., personal communication). Surface circulation is driven on short time scales (hours to days) by local winds and on longer time scales (weeks to months) by density driven exchanges with shelf waters and the inshore branch of the Labrador Current (deYoung and Sanderson 1995; deYoung et al. 1993*b*). As well, storms can generate Kelvin waves trapped within about 5 km of either coast whose associated currents have a jetlike character (deYoung et al. 1993*b*). Water properties are similar to those found offshore in the open ocean. Stratification is primarily due to salinity with some thermal effect in the upper 10–20 m. Subzero temperatures are typically found below 50 m. Mixed layer depths range from about 10 to 40 m.

Survey design and sampling procedures

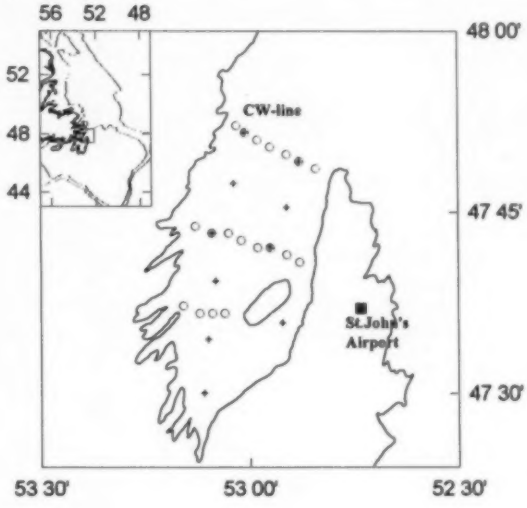
Surveys were conducted in the summers of 1990 (June 25 to July 16) and 1991 (July 3 to July 17) as indicated in Fig. 1. The surveys were designed to (1) estimate the abundance of ichthyoplankton populations in the inner portion of the bay at regular intervals and (2) provide simultaneous observations of water properties (temperature, salinity) as

well as currents throughout the bay to estimate the fluxes of organisms across the mouth of the bay. In 1990, biological and physical measurements were made from a single vessel (CSS *Shamook*), and surveys of larval concentrations and currents within the bay (that is, interior to CW-line (Fig. 1)) were alternated with estimations of the fluxes across the CW-line. A single transect of CW required about 5 h (27 June, 3, 12, and 15 July). Complete surveys of the inner bay were conducted every 6–7 d (28–29 June, 3–4, 11, 13, and 16 July). Ship failure caused a relatively long, 6-d gap in midprogram (5–10 July); shorter gaps were due to weather conditions. In 1991, the addition of a second vessel, CSS *Marinus*, permitted almost daily estimates of the fluxes of water and larvae across CW (4–8 and 10–14 July); larval abundance within the bay was estimated every 6 days (3, 9, and 15 July). Biological and water property measurements were made from *Marinus*, whereas *Shamook* was devoted to current measurements. Transects of CW-line were carried out nearly simultaneously by both ships, and the time required to measure currents along a single transect was reduced to less than 2 h. Ichthyoplankton sampling along the CW-line still required approximately 4 h.

All sampling was conducted during daylight hours (07:00–19:00) to avoid potential bias associated with diurnal variations in net avoidance. None of the species considered in the following analysis exhibited any precipitous changes in abundance with increased size (Pepin 1993), which would be indicative of length related increases in avoidance. Ichthyoplankton samples were obtained using a 4-m^2 Tucker trawl equipped with sections of 1000-, 570-, and 333-μm mesh Nitex. At each station, a single oblique tow of approximately 15 min was made at 2 knots (1 $m \cdot s^{-1}$). The net was lowered to 40 m and retrieved at rates of 0.25 $m \cdot s^{-1}$ and 0.064 $m \cdot s^{-1}$. Maximum tow depth was chosen to include the mixed layer in which >95% of the larval fish reside (Frank and Leggett 1982; deYoung et al. 1994; J. Anderson, Northwest Atlantic Fisheries Center, St. John's, Nfld., personal communication). Volumes filtered were estimated from the average of two General Oceanics flow meters positioned at the mouth of the net to avoid possible errors due to malfunctions; abrupt changes in the difference in flow rates were considered to be indicative of blockage in one instrument. On deck, the net was washed and the samples were preserved in 2% buffered formaldehyde.

Currents were measured with a 153 kHz RD Instruments acoustic Doppler current profiler (ADCP) as described in Colbourne et al. (1993). In 1990, the ADCP was operated in bottom track mode at ship speeds up to 4 knots (2 $m \cdot s^{-1}$); data were recorded in 4-m depth intervals (first bin: 5–9 m) using a sampling interval of 1 min giving along-track ensemble lengths up to 120 m. The standard deviation of unsmoothed single bin currents was about 0.10 $m \cdot s^{-1}$. In 1991, the sampling interval was lengthened to 3 min (up to 720 m along track) and the ADCP was housed in a hydrodynamically designed mount that reduced the single bin standard deviation to 0.03–0.05 $m \cdot s^{-1}$ and allowed operation speed to be increased to a maximum of 8 knots (4 $m \cdot s^{-1}$) (Colbourne et al. 1993).

Fig. 1. Conception Bay, Newfoundland, Canada, showing station location sampled in 1990 (circles) and 1991 (crosses). The transect of seven stations located at the mouth of the bay is herein referred to as the CW-line. The location of the weather station at St. John's Airport is also indicated.



Salinity and temperature profiles were made at each net station to within 5 m of the bottom using a Seabird-19 (1990) or Seabird-25 (1991) conductivity–temperature–depth (CTD) meter. The conductivity and temperature sensors of both instruments were calibrated under laboratory and field conditions.

Laboratory analysis

Ichthyoplankton were sorted and identified to species or the lowest taxonomic level possible by the Atlantic Reference Centre (Huntsman Marine Science Centre, St. Andrews, N.B.). Subsampling of an individual taxon was performed for samples in which numbers of that species exceeded 200 individuals per stage (i.e., eggs or larvae) using a beaker technique (van Guelpen et al. 1982). The length frequency distribution for each species and sample was estimated by measuring up to 200 larvae. Standard length was measured to the nearest millimeter using a dissecting microscope and a gridded background. Abundance (number per 1000 cubic metres) was calculated for each species for every 1-mm length interval for each sample. Abundance estimates were corrected for the number of larvae that could not be measured due to damage (<5%).

Changes in abundance

The temporal changes in the abundance of fish larvae in Conception Bay in 1990 and 1991 were estimated for each species. The daily abundance estimate of each species was calculated by summing estimated abundances for each length interval over all stations with positive catches and dividing by the total number of stations sampled that day in the inner portion of the bay. Estimates of total abundance were obtained by multiplying concentrations (number

per 1000 cubic metres) by the area of the bay. The average rate of change in abundance for each species and year was estimated using an exponential model

$$[1] \quad N_t = N_0 e^{-Mt}$$

where N_t and N_0 are the average number of larvae per 1000 cubic metres at times t and 0, t is time (days), and M is the average rate of change in abundance (1/days). M is equal to the sum of natural mortality (Z) and physical fluxes (F), which can result in either immigration or emigration. The average number of larvae at the start of the survey (N_0) represented the total number of larvae caught (i.e., all size categories combined). Subsequent estimates of N_t were obtained by summing the abundance of larvae of a size equal or greater to the projected size at time t of the smallest length category caught during the first survey ($t = 0$). Growth rates were estimated for each species using a modal analysis (e.g., MacDonald and Pitcher 1979) modified to take into account variations in egg production for pelagic spawners or the production of the smallest size class of larvae for demersal spawners. The model (Eq. 1) was fit by regressing the $\log_e(N_t)$ in relation to t. Each estimate of abundance (N_t) was weighted by the inverse of the log-transformed estimated sample standard deviation ($\log_e(s_t)$) of the estimated larval abundance at time t to normalize to a common variance scale. We combined the estimates of abundance (N_t) for all species into an analysis of covariance (ANCOVA) model with species as a categorical variable. This provided a more precise estimate of M because treating individual species as independent observations increased sample size. To determine whether a common average daily rate of change in abundance for different species in the bay (i.e., slope) was a reasonable model, we included an interaction term (species × time) in the model. If the interaction term was significant ($P < 0.05$), M was estimated for individual species using a general linear model.

Flux estimates

Point estimates of the upper layer volume transport F_W (cubic metres per day) across CW-line for each ADCP ensemble were made by first rotating the measured currents (metres per second) 25° clockwise to align them with the general axis of the bay, summing the along-bay flow over the upper nine bins (5- to 41-m depth), and multiplying by the along-track length of the ensemble (metres). Larval abundance fluxes F_L (larvae per day) were computed as weighted sums over m tows:

$$[2] \quad F_L = \sum_{n=1}^{m} N_n \sum F_{Wj}$$

where N_n is the larval concentration estimated from the nth tow; F_{Wj} is the along-bay volume transport of water in the jth ADCP ensemble, and the sum over ensembles extends between midpoints separating tows. In all but one case, seven stations, each 2–4 km apart, were occupied on each CW transect. The volume transport was standardized relative to the volume of the upper layer in Conception Bay, $V = 40 \text{ m} \times 10^3 \text{ km}^2 = 4 \times 10^{10} \text{ m}^3$ so that it is expressed as a renewal rate (1/days). Given the variances of the single ensemble – single bin velocity measurements, we estimate the maximum standard deviation in volume transport is $0.008 \cdot d^{-1}$ in 1990 and $0.002–0.004 \cdot d^{-1}$ in 1991, much smaller than the typical magnitude of F_L in Conception Bay.

Although tidal currents are weak in Conception Bay, their integrated effect can be significant. They were estimated and removed from the flux calculations as follows. The tidal flow was treated as homogeneous and simultaneous over the bay as well as depth independent. The tidal height (range ~1 m) was predicted at the time of each ADCP ensemble using known harmonic constants (Canadian Hydrographic Service, Ottawa, Ont.) and the requisite hourly volume transport calculated and converted into an along-bay velocity by dividing by the length and mean depth of the transect. The observed current velocity was then corrected for the contribution of the tidal current.

Larval abundance fluxes across the mouth of the bay were estimated for each species and each length interval. Between surveys, the net daily flux of each species was estimated by summing the net transport across the mouth for all appropriate length categories for each day the CW-line was occupied. Length categories included in the estimate of net fluxes consisted of those equal to or greater than the smallest size category, projected using the growth model, which were included in the estimate of total population abundance at the start of each survey period. Fluxes of larval fish were standardized relative to total abundance of larvae at the start of each survey period ($F = F_L/(N_i V)$).

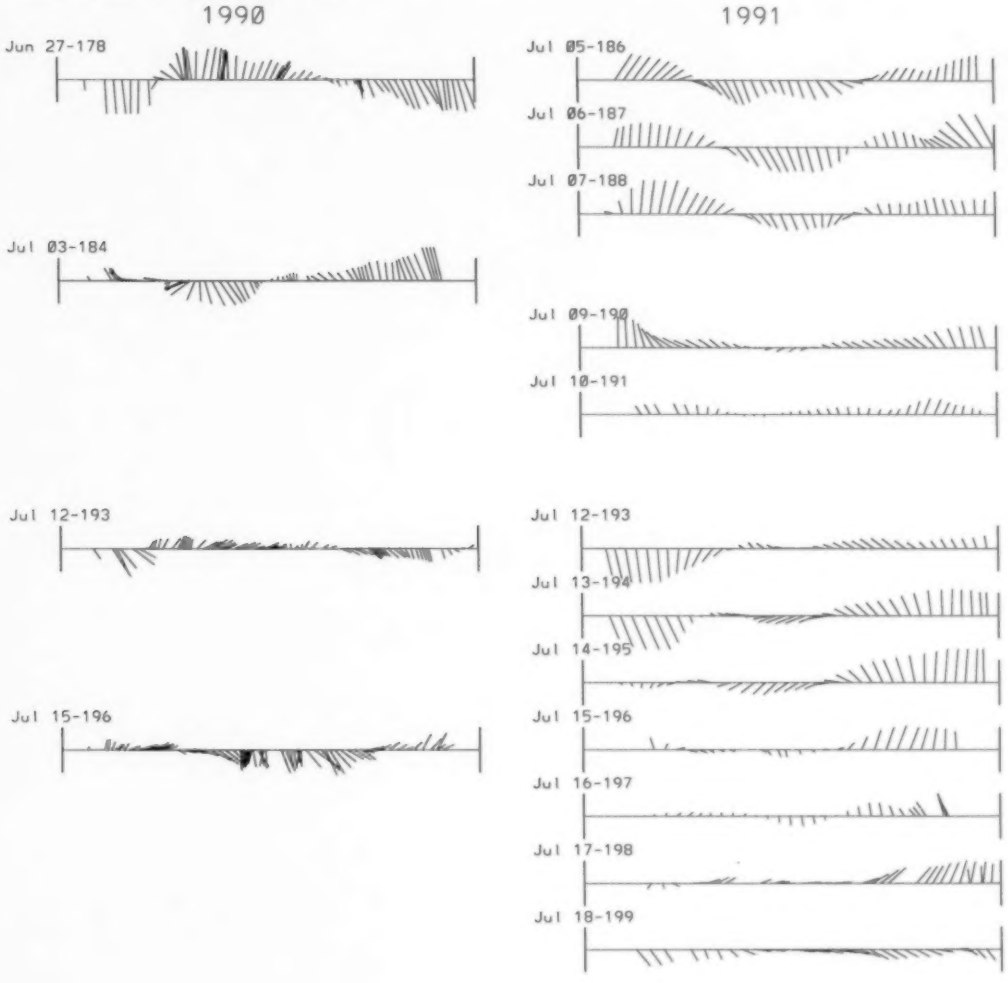
Results

General circulation features

Circulation at the mouth of Conception Bay varied significantly between and within years, largely because of differences in wind forcing. Nonetheless, there were similarities in the 2 years as revealed by the time series of currents across CW-line (Fig. 2). Several features are evident, the most prevalent being an outflow along the eastern shore that is visible in 13 of the 16 transects. Fully 75% of the observations (12 of 16) exhibit a pair of nodes at which the current reverses direction. This suggests a length scale of about 5 km, roughly the first Rossby internal deformation radius and similar to the decorrelation scales reported by deYoung and Sanderson (1995). The circulation feature that most greatly distinguishes the two years is the occurrence in 1990 of two of the three patterns in which there is an inflow along both coasts and a strong to weak outflow in the centre that leads to a net influx of water into the bay in the upper layer. Four transects display a single node pattern, all with outflow along the eastern shore.

In both years the prevailing wind was from the southwest (out of the bay). The study period in 1990 was marked by a series of relatively strong disturbances about 8 d apart during which the wind stress peaked at close to $0.1 \text{ N} \cdot \text{m}^{-2}$ out of the bay (Fig. 3). These events were followed by weaker, but significant, in-bay winds, characteristic of storms that track through the region at this time of year. In 1990, the net flux of water across CW-line at the end of each of the two sampling periods was roughly inverse to

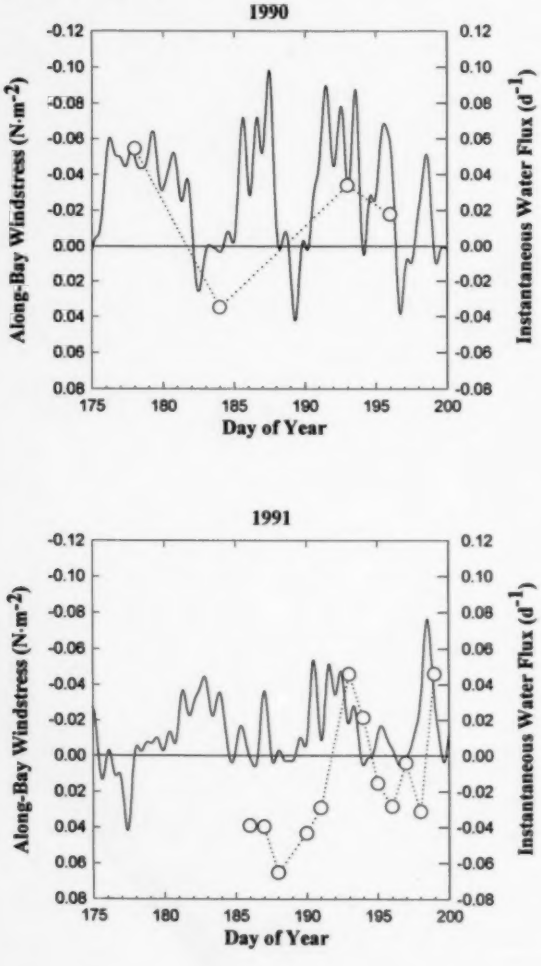
Fig. 2. Upper layer currents along the CW-line in Conception Bay in 1990 and 1991. The currents have been averaged over the upper 41 m of the water column, smoothed, and rotated by 25° to align with the major axis of the bay so that a vector pointing toward the top of the page is out of the bay. The end bars of each panel correspond to a speed of 0.20 $m \cdot s^{-1}$.



that at the beginning as the system shifted from out-bay to in-bay winds (Fig. 3). By contrast, 1991 was much calmer, as weaker out-bay episodes were followed by very weak in-bay winds. During the first leg (days 184–190, 1991), wind shifts had little effect on the daily net flux of water and the average outflow was 4.6%·d^{-1}. Fluxes during the second leg (days 191–197, 1991) changed markedly as a relatively weak disturbance moved through the area. A strong in-bay flow along the northwest coast led to a net influx during the period of weak winds, although the overall pattern suggests some of the inflow could have been recirculated water that originated in the persistent flow along the southeastern coast (Fig. 2). This inflow diminished as winds turned out-bay, leading to an average influx of only 0.5%·d^{-1} during the second leg (Fig. 3). Overall, the average net daily flux ranged from an influx of 5.8%·d^{-1} to an efflux of 6.2%·d^{-1}.

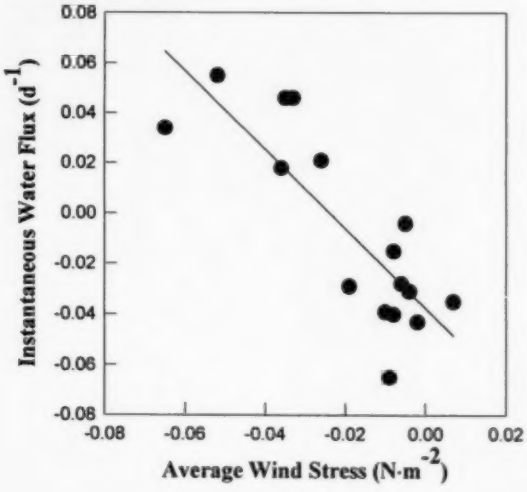
The daily flux of water in the upper 40 m shows a highly significant association with the average wind stress averaged over the 48 h preceding each measurement ($F_{1,15}$ = 30.9, $p < 0.001$, $r^2 = 0.69$, $F_w = -0.037 - 1.57\ W_{48}$, where F_w is the instantaneous water flux and W_{48} is the average hourly wind stress during the previous 48 h; the standard errors of the intercept and slope are 0.008 and 0.29, respectively) (Fig. 4). At first sight, this relation appears counterintuitive as an out-bay wind forces an in-bay current, and it does, indeed, differ from common notions of the steady state response of bays to winds (Csanady 1982; Greatbatch and Otterson 1991). However, the upper layer response of Conception Bay to winds depends strongly on

Fig. 3. Net daily instantaneous flux of water along the CW-line during each of the two surveys for 1990 and 1991 (circles) and the low-pass filtered along-bay wind stress (solid line). Hourly winds measured at St. John's airport were converted to wind stress using the Large and Pond (1981) wind-speed variable drag coefficient formulation, rotated clockwise by 25° to align with the mean bay direction, and run through an 8th order Butterworth filter that passes 95% of variability with periods greater than 24 h and damps 97.5% of the variance with periods less than 16 h. St. John's airport is about 15 km east of Conception Bay on the Atlantic coast, and is the sole source of reliable wind data. Negative along-bay wind stress corresponds to winds blowing out of the bay. Note that the *y*-axis for wind stress is reversed.



the set-up and relaxation of sea level and pycnocline slopes and their spatial distribution, which in turn depend on bay geometry and the wind history. In addition, deYoung et al. (1993*a*) have shown upstream forcing generated in other bays and coastal waters to be important. A more complete understanding of physics underlying this statistical relationship is the goal of an ongoing investigation.

Fig. 4. Relationship between the instantaneous water flux in the upper 40 m of the water column, measured along the CW-line, and the average hourly windstress during the preceding 48 h. Data for both 1990 and 1991 were included in the analysis.



Changes in abundance

Ichthyoplankton catches in 1990 and 1991 included 24 and 26 species, respectively. Only five species in 1990 and six species in 1991 were present in sufficient numbers to accurately estimate average daily rates of change in abundance throughout the survey periods (Table 1). Species used in this analysis occurred in an average of 94% and 78% of all samples in 1990 and 1991, respectively. Despite the high occurrence of these species, the average abundance (larvae per 1000 cubic metres) of the species used in the analysis was substantially higher in 1990 (range of means: 3–107) than in 1991 (range of means: 2.4–6.6). The major differences in species composition and length–frequency distributions between years (Table 1) appear to have been caused by colder than normal conditions in 1991, which resulted in a delay in spawning activity for many species (Laprise and Pepin 1995).

Average daily rates of change in abundance varied between years (ANCOVA, $F_{1,46} = 5.8$, $P < 0.05$) (Fig. 5). The weighted ANCOVA did not reveal a significant interaction in the rate of loss among species in 1990 ($F_{4,28} = 0.74$, $P > 0.5$). The average total rate of loss estimated for all species was $M = 0.11 \cdot d^{-1}$ (SE = 0.013, $P < 0.001$). In 1991, the analysis of covariance did not show evidence of a strong interaction among species ($F_{5,17} = 0.12$, $P > 0.5$). The estimated rate of loss representative of all species was $M = 0.048 \cdot d^{-1}$ (SE = 0.022, $P < 0.05$).

Larval fluxes

In both years, the fluxes of larvae into or out of Conception Bay closely followed variations in the flux of water (Fig. 6). Estimated daily fluxes of fish larvae were correlated with

Table 1. Percentage of samples in which the dominant species occurred and length intervals used in this study.

Year	Species	Occurrence (%)	Length interval (mm)	Estimated growth rate ($mm \cdot d^{-1}$)
1990	*Gadus morhua*	99	3–16	0.33
	Hippoglossoides platessoides	100	3–15	0.34
	Liparis atlanticus	94	3–8	0.07
	Pleuronectes americanus	76	2–6	0.22
	Ulvaria subbifurcata	99	4–13	0.38
1991	*Boreogadus saida*	80	7–18	0.42
	Hippoglossoides platessoides	63	4–11	0.33
	Liparis gibbus	87	7–19	0.29
	Lumpenus sp.	88	10–25	0.12
	Stichaeus punctatus	78	10–18	0.25
	Ulvaria subbifurcata	72	4–11	0.17

the instantaneous water flux ($r^2 = 0.38$, $P < 0.001$, $n = 66$) but the slope and intercept did not differ significantly from 1 ($t = 1.22$, $P > 0.1$) and 0 ($t = 1.58$, $P > 0.1$) respectively. Furthermore, there were no significant differences in flux rates among species (ANCOVA, $F_{9,65} = 1.2$, $P > 0.1$). General differences in the distribution of estimated fluxes of larvae between years reflect variations in oceanographic conditions, as they are influenced by short-term variations in wind forcing, and to a lesser extent by spatial variations in larval production patterns for species included in our analysis (P. Pepin, unpublished data). It is not possible to accurately estimate the overall flux of larvae for 1990 because of the limited sampling possible during that year (see below). For 1991, the average efflux of fish larvae estimated from the observations made along the CW-line during our survey was $3.7\% \cdot d^{-1}$, which is approximately equal to the average daily rate of change in abundance estimated for that period.

Larval flux measurements are subject to several sources of error related to the vertical distributions of currents and larvae. The tows were designed to survey the full depth occupied by the larvae, and there is little likelihood that significant numbers were found deeper than 40 m given the temperature and stability profiles of the water column. However, if larvae were uniformly restricted to lesser depths, our estimates would be biased low because the predominately wind driven currents are usually sheared vertically with their maximum speeds at the surface. That is, the appropriate upper layer current would be underestimated. In this respect, the estimates of the transport induced contribution to apparent mortality quoted here should be regarded as a lower limits. We note, however, that the physical situation is one characterized by significant variability in current shear as a comparison of ADCP sensed subsurface currents with surface currents monitored by high-frequency radar shows (J. Helbig, unpublished data). In fact, there even exist brief periods when surface currents are opposite in direction to those at depth. In these cases a subsurface current maximum is often observed. Notwithstanding this caution, however, we must defer examination of effects of vertically sheared currents on larval transport until further field work is carried out to determine the vertical distribution of larvae.

Of potentially greater significance would be a bias in the vertical distribution of larvae between incoming and outgoing flows. Suppose, for example, that the currents were vertically sheared, decreasing away from the surface and that the outflowing currents were associated with thinner mixed layer than were incoming flows. Then the estimated net efflux of larval from the bay would be underestimated. To test for this possibility, we examined the relationship between the estimates of volume transport and mixed layer depth at the intervening CTD station. These measures included the depths of the 2, 1, 0, and $-1°C$ isotherms and the depth of the maximum Brunt–Väisälä (stability) frequency. If such a bias were present, one would expect to find a statistically significant relationship between currents and trapping depth. No correlation was found in any case ($r^2 \approx 0.01$) as illustrated in Fig. 7, and we conclude that this type of bias is unimportant.

Discussion

Most of our knowledge about how the distribution of planktonic organisms is affected by ocean currents is based on assumed steady-state or average conditions (Power 1986; Bartsch et al. 1989). Indicator species provide some information about variations in the exchange between water masses but relatively little is known about the contribution of physical fluxes to population processes (Bakun and Parrish 1982; Taggart and Frank 1990). Our results provide evidence of the potential significance of immigration and emigration from an area to the study of natural mortality. Most important, however, is that the correction introduced into estimated mortality rates by physical fluxes can vary from day to day and between cohorts or year-classes. The consequences of such fluctuations in the contribution of transport processes to changes in population

Fig. 5. Temporal changes in the average abundance of fish larvae in Conception Bay in 1990 and 1991 for the species listed in Table 1. The upper and lower case letters in each symbol represent the genus and species names.

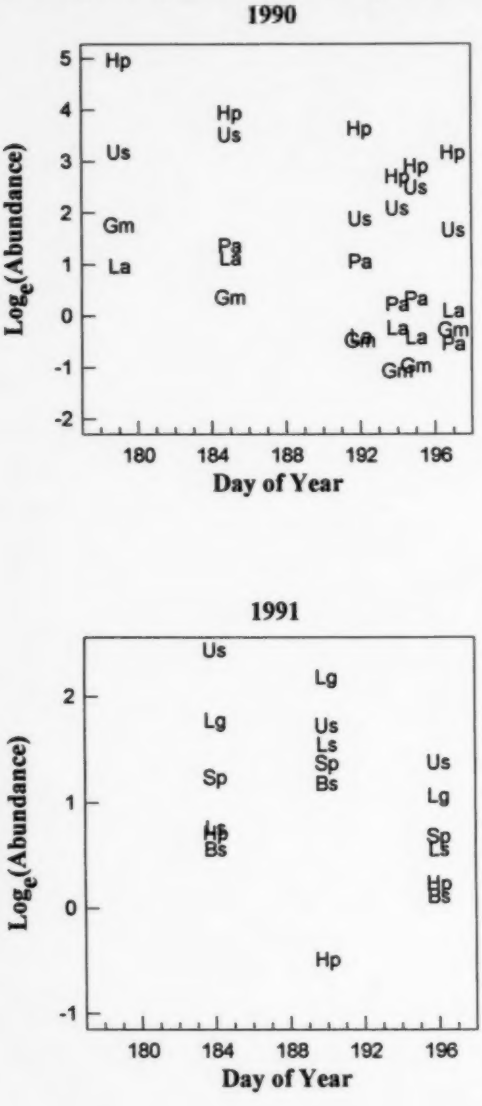
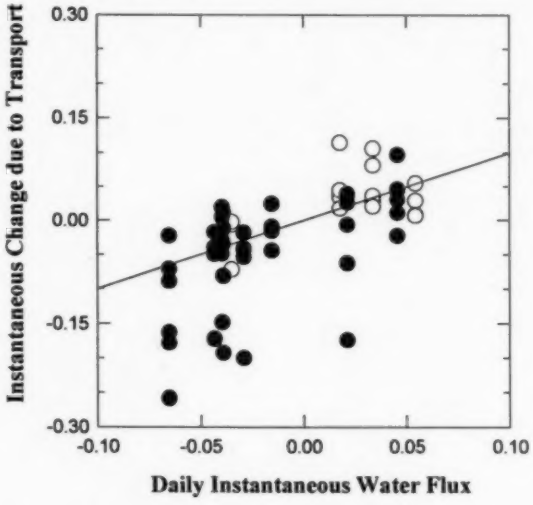


Fig. 6. Daily instantaneous fluxes of fish larvae attributable to transport at the mouth of Conception Bay in relation to the net daily instantaneous water flux estimated from our surveys. Positive values indicate inflow, negative values represent outflow. Open symbols represent estimates for the 1990 surveys and closed symbols represent estimated for the 1991 surveys. Each symbol represent the estimated daily flux of individual species used in our analysis. The regression describing the data (not shown) is $Y = -0.012 + 1.24X$, where Y is the change in population abundance attributable to transport, X is the instantaneous exchange of surface waters in the bay, and the standard errors of the intercept and slope are 0.0078 and 0.19, respectively. The reference line is provided to indicate values at which the daily proportional exchange of larvae is equal to the daily proportional exchange of water.



abundance of larval fish in a sampling area are substantial. For example, emigration from the study region in 1991 accounted for approximately 75% of total losses; ignoring it would have led us to overestimate biological losses by more than a factor of four. Calculations by Houde (1987) and Beyer (1989) clearly show that for organisms with average instantaneous mortality rates of the order of $0.10 \cdot d^{-1}$, periodic or prolonged variations of ±10% in mortality rates could result in changes in survival approximating the magnitude of fluctuations in observed recruitment. It is evident that changes in larval abundance attributable to physical processes could seriously bias predictions and understanding of the factors contributing to variations in abundance, as others have observed (e.g., Taggart and Leggett 1987).

However, it is not sufficient to simply consider the average contribution of physical processes to population dynamics because our results point to the potential significance of short-term variations in transport of fish larvae. Estimates of residence times based on a steady-state diagnostic model of Conception Bay suggests that 2.3% of the surface layer would be exchanged daily, resulting in a corresponding loss of larvae if production was restricted to the inner portion of the bay (deYoung et al. 1994). Although this may appear reasonable given the average circulation pattern, short-term variations in transport can be of greater magnitude than the predicted mean. Specifically, our results show that currents at the mouth of Conception Bay respond to variations in wind forcing on a time scale of about 1 d. Failure to account for such variations would lead to inaccurate forecasting of survival, particularly if the coincidence between biological and physical events varies randomly. Although we have gained some qualitative

Fig. 7. Scatterplot of along-bay current with the mixed layer depth as estimated by (A) the 1°C isotherm and (B) the depth of the maximum Brunt–Väisälä N^2 frequency squared. Speeds are in metres per second, depths in metres, and N^2 in 1/second^2.

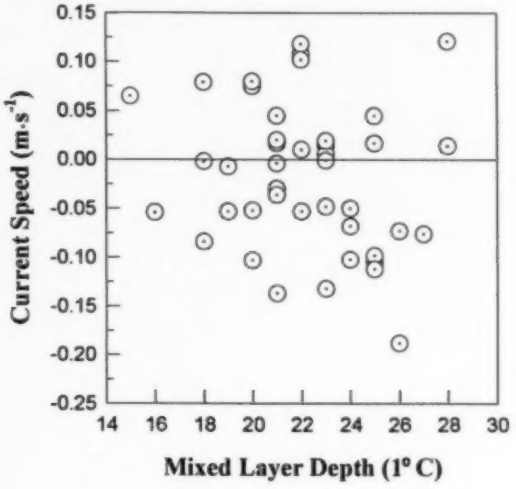
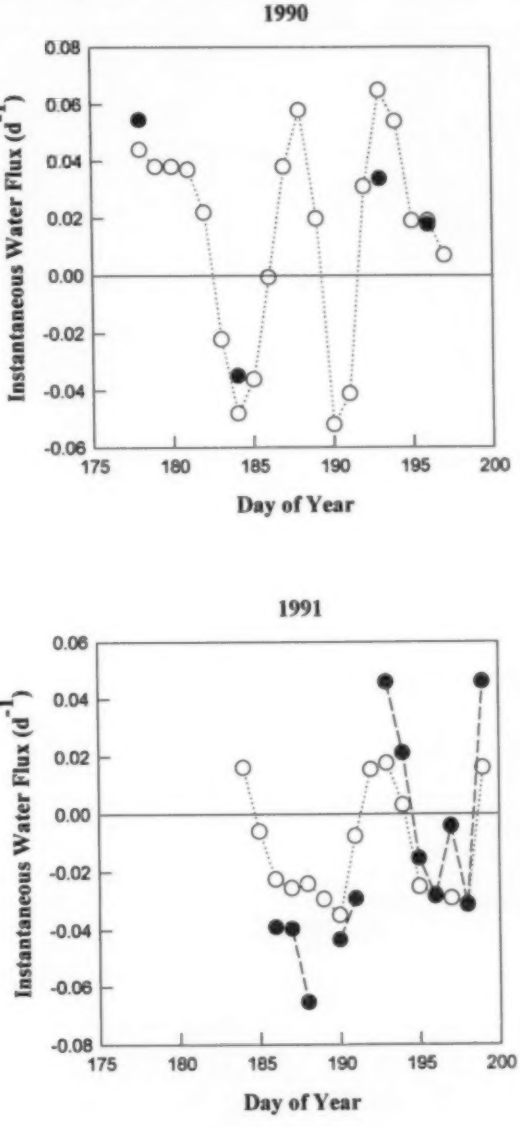


Fig. 8. Predicted (open circles) and observed (solid circles) water fluxes at the mouth of Conception Bay. Predictions are based on the windstress-water flux relationship reported in Fig. 4.



understanding about the effect of wind forcing on circulation in Conception Bay, our predictive capability remains limited.

The precision of estimated fluxes is limited by both biological sampling variability and by short-term fluctuations in physical processes. Both these factors are evident when we contrast the larval–water flux relationship (Fig. 6) and the variations in the wind-related forcing of water flux at the mouth of Conception Bay (Fig. 8). The consequences of limited sampling can be substantial. Given the high short-term, wind-related variability in water fluxes found in this study, mean estimates of larval fluxes based on few observations may be biased because of aliasing. The magnitude of this bias depends, in part, on the length of the time intervals between each estimate of larval fluxes and the period between estimates of abundance in the study area. Our results in 1990 illustrate the effects of temporal aliasing on the estimation of average larval fluxes. Whereas physical fluxes predict an average daily influx of 1.3% (Fig. 8), the average larval fluxes estimated from our observations would indicate an average daily influx of 3.7%. As a result, the contribution of transport to changes

in population abundance would be overestimated by a factor of three (12 vs. 34% of the average daily change in abundance), and biological losses would be underestimated. The addition of sampling variability could substantially increase the error associated with the estimated fluxes. It is evident that high-frequency sampling is needed to resolve the variability in physical processes and to reduce the sampling error to obtain an accurate perspective of the magnitude of changes in abundance resulting from physical and biological processes.

Both measurements of larval fish abundance in the bay and larval fluxes across the mouth are influenced by ichthyoplankton distribution. Spatial coverage and the sample size influence the precision of our observations. The average decorrelation length scale in sample abundance is approximately 5–10 km in Conception Bay but this varies with the stage of development and the overall abundance of each species (P. Pepin, unpublished data). The lack of independence in the observations along each transect in 1990 (stations 2–3 km apart) may bias estimates of the variance in average abundance of larvae. The problem should not be important in 1991 when stations were spaced approximately 10 km apart (see Cochran 1977). However, because the average daily rates of change in larval abundance are substantially different between years and because there is no apparent difference among species within years, the bias in estimated sample variance is unlikely to significantly influence the conclusions of our study. It is clear that increasing sample size would have increased the precision of our estimates of abundance (Cyr et al. 1992). However, our objective was to achieve an accurate representation of the system's dynamics by monitoring processes through frequent surveys of both the bay and its open boundary. This may be particularly important when both demographic and transport processes are highly variable in time and space (Horne and Schneider 1994). Precision was achieved by combining observations from several species. We estimate that the 95% confidence intervals of the average daily flux of larvae is approximately $\pm 1.5\%\cdot d^{-1}$. Although this is large relative to the average fluxes estimated, information from individual species would have yielded substantially larger errors resulting from sampling variability (Fig. 6). Our sampling design was aimed at maximizing the temporal resolution with a concomitant reduction in the precision of any single estimate. Careful consideration of the spatiotemporal resolution of sampling programs for organisms with high turnover rates represents one of the fundamental issues that need to be addressed to gain proper understanding of processes affecting fish populations during the early life stages.

The absolute magnitude of changes in abundance attributable to advection and diffusion of larvae in our study area ranged from nearly 0 to more than $6\%\cdot d^{-1}$ (the overall absolute average instantaneous flux is $0.037\cdot d^{-1}$, combining both years) and are within the range of observations from other studies. Taggart and Leggett (1987) measured an average instantaneous transport rate of approximately $0.3\cdot d^{-1}$. An estimate based on McGurk's (1989) study of Bamfield Inlet and Trevor Channel yields an instantaneous transport of $0.1\cdot d^{-1}$. Kim and Bang (1990) obtained a correction of $0.016\cdot d^{-1}$ for the physical loss of larvae from Shelikof Strait. Although few in numbers, these values give some indication that real or apparent advective and diffusive effects may be scale dependent (Fig. 9). Intuitively, small systems, such as Bryant's Cove studied by Taggart and Leggett (1987), will be flushed more rapidly than a larger system such as Conception Bay and, thus, will be more susceptible to short time scale physical variability.

To make this notion more concrete, consider a region of area A enclosed by a coastline of length l_c and an open boundary of extent l_o. The equation for the instantaneous rate of change of the space and time varying abundance $N(x,y,z,t)$ expresses a balance between natural mortality, horizontal and vertical advection, and horizontal and vertical diffusion:

$$[3] \quad \frac{\partial N}{\partial t} = ZN - u\cdot\nabla_H N - w\frac{\partial N}{\partial z} - K_H\nabla_H^2 N - K_V\frac{\partial^2 N}{\partial z^2}$$

where u and w are the respective horizontal and vertical velocities, ∇_H is the horizontal gradient operator, and K_H and K_V are the horizontal and vertical diffusivities. We integrate Eq. 3 over the upper layer depth D and the area A to obtain

$$[4] \quad \frac{\partial \bar{N}}{\partial t} = -Z\bar{N} - \frac{1}{A}\int_{open}\hat{u}_\perp\hat{N}_o ds - \frac{K_H}{A}\int_{open}\frac{\partial \hat{N}_o}{\partial s_\perp} ds$$

where $\bar{N}(t)$ is the mean particle concentration in the upper layer, $\hat{N}_o(s,t)$ is the depth averaged concentration along the open boundary, and $\hat{u}_\perp$ and $\partial\hat{N}_o/\partial s_\perp$ are the depth averaged current and the concentration gradient normal to the open boundary. The terms in Eq. 3 that express the vertical advection and diffusion of larvae vanish as D is assumed large enough so that N is essentially zero at the bottom of the mixed layer.

We estimate the correction to the instantaneous mortality rate due to advection and diffusion as

$$[5] \quad F \sim \frac{l_o\hat{u}_\perp\hat{N}_o}{A\bar{N}} + K_H\frac{l_o\partial\hat{N}_o/\partial s_\perp}{A\bar{N}}$$

$$\sim \frac{\hat{u}_\perp}{l_c}\left[1 + O\left(\frac{K_H\partial\hat{N}_o/\partial s_\perp}{\hat{u}_\perp\hat{N}_o}\right)\right]$$

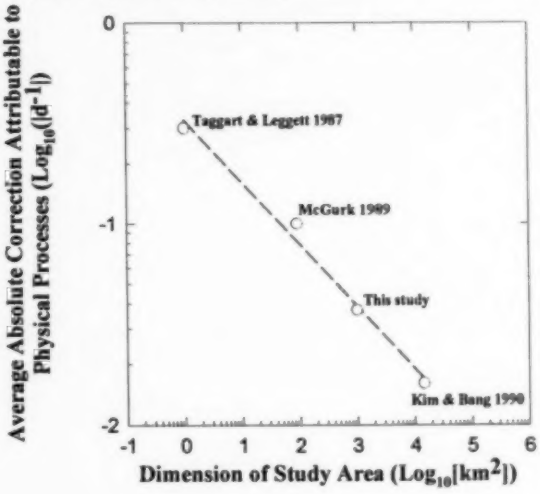
$$\propto A^{-1/2}$$

where we have approximated $A \sim l_c l_o \sim l_c^2$ and where $O(\cdot)$ indicates the size of the diffusive term relative to the advective term. The diffusive term in Eq. 5 is generally much smaller than the advective one since the concentration gradient tends to be small across the boundary. Typically, $K_H \sim 50\ m^2\cdot s^{-1}$, $\hat{u}_\perp \sim 0.1\ m\cdot s^{-1}$ so that

$$[6] \quad \frac{K_H\partial\hat{N}_o/\partial s_\perp}{\hat{u}_\perp\hat{N}_o} \sim \frac{500\ m}{L_o}$$

where L_o is the length scale characteristic of changes in $\hat{N}$ at the boundary. Thus unless L_o is of the order of about a kilometre or less, diffusive effects are small compared with advective ones. In other words, unless the open boundary is frontal in nature and exhibits an extreme gradient in $\hat{N}$, the effect of diffusion on the total number of larvae can be ignored in a semienclosed system to first order.

Fig. 9. Logarithmic representation of the absolute value of the average instantaneous rate of change in larval abundance attributable to physical processes (1/days) in relation to the dimension of the study area (square kilometres) for four studies conducted according to a fixed grid survey design. Values from this and Taggart and Leggett's (1987) studies represent possible increases or decreases in population abundance attributable to physical fluxes of animals from the study areas whereas McGurk (1989) and Kim and Bang (1990) only reported decreases in population abundance because of advection or diffusion. Patch studies were excluded from this analysis because each survey is adapted to follow the movement of a concentration of larval fish. Such a scheme does not consider changes in abundance with respect to specific study areas per se.



The best straight line through the four estimates in Fig. 9 has a slope of nearly $A^{-1/3}$, roughly agreeing with our relatively crude estimate. This is not surprising because Eq. 5 enjoys a very simple physical interpretation. Specifically, our approach merely quantifies in an approximate sense our intuitive notion that small systems flush quickly by providing an estimate of the fractional renewal of the upper layer volume per unit time ($Q = Dl_o\hat{u}_\perp/DA$). In fact, given estimates of the mean influx or efflux rate, $\hat{u}_\perp$, Eq. 5 allows us to estimate the maximum time interval between full bay larval surveys required to keep the error in $M = (Z + F)$ resulting from physical processes (F) below some specified value. Equation 5 defines a time $T = A/\hat{u}_\perp l_o$ over which the correction to M will be the same size as M itself. For example, for Conception Bay, 0.04 $m \cdot s^{-1}$ is a reasonable estimate for $\hat{u}_\perp$ yielding $T \sim 17$ d. Thus, our survey interval of 6 d translates into an approximate correction of 35% to the total change in abundance, which is of the same order as the range of values estimated in 1990 and 1991. This estimate does not explain the results of 1990, however. Indeed, the mean currents across CW in 1990 were smaller than those measured in 1991 suggesting a greater insulation to apparent changes in abundance. Clearly other processes, e.g., storms, were at play. In this regard however, Eq. 5 also quantifies the susceptibility of small systems to error introduced by short-term physical forcing. A temporary increase in the boundary flux $\hat{u}_\perp$ can lead to an appreciable volume transfer Q, if A is relatively small.

Despite differences in average mortality rates and estimated fluxes between the two years, there was no evidence of significant differences among species within years. This is somewhat contrary to what one might expect because of differences in size (e.g., Houde 1989; Morse 1989; Pepin 1991) or other potential differences in early life history (e.g., spawning behaviours, swimming abilities). General principles are often derived from comparisons of species from different study sites or that were segregated in time (e.g., Morse 1989). All species considered in our analyses were sampled over the same period. Furthermore, work by Laprise and Pepin (1995) dealing with the spatiotemporal occurrence of ichthyoplankton in Conception Bay supports Frank and Leggett's (1982) suggestion that many species of fish release their eggs and larvae in the same water masses, presumably to take advantage of particular conditions that enhance growth and survival through the larval stage. Our results lend some support to this hypothesis in that we were unable to measure significant differences in population dynamics among the various species. Further research is required to determine whether the similarity among species is due to exposure to similar environmental conditions or that the net effect of different factors leads to similar rates of change in abundance.

To summarize, our estimates of the effects of physical processes appear to be reasonable for moderate-sized regions like Conception Bay where currents and larval abundances can be monitored frequently relative to the physical exchange rates. In smaller areas, monitoring physical changes may be more difficult because of high variability in currents. Conversely, accurate synoptic surveys of populations distributed over large domains may be equally difficult to achieve. It is clear that, under any circumstance, the contribution of physical processes can bias estimates of mortality rates, whether transport results in net immigration or emigration from the system, as suggested by Taggart and Leggett (1987). Measurements of the effect of physical processes are essential to properly investigate the causes of variations in ichthyoplankton population dynamics. However, as our comparison with other studies suggests, the relative magnitude of the contribution of physical processes to variations in population abundance are likely to be scale dependent.

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References

Bailey, K.M. 1981. Larval transport and recruitment of Pacific hake. Mar. Ecol. Prog. Ser. 6: 1–9.

Bakun, A., and R.H. Parrish. 1982. Turbulence, transport and pelagic fish in the California and Peru Current systems. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 99–112.

Bartsch, J., K. Brander, M. Heath, P. Munk, K. Richardson, and E. Svendsen. 1989. Modelling the advection of herring larvae in the North Sea. Nature (London), 340: 632–636.

Beyer, J. 1989. Recruitment stability and survival: simple size-specific theory with examples from the early life dynamics of marine fish. Dana Rep. Carlsberg Found. 7: 45–147.

Cochran, W. G. 1977. Sampling techniques. 3rd ed. Wiley, New York. 428 p.

Colbourne, E.B., J.A. Helbig, and D. Cumming. 1993. Improved ADCP performance using a hydrodynamically designed boom mount. J. Atmos. Oceanic Technol. 10: 629–636.

Csanady, G.T. 1982. Circulation in the coastal ocean. D. Reidel Publishing Company, Amsterdam. 274 p.

Cyr, H., J.A. Downing, S. Lalonde, S.B. Baines, and M.L. Pace. 1992. Sampling larval fish populations: choice of sample number and size. Trans. Am. Fish. Soc. 131: 356–368.

deYoung, B., J.T. Anderson, R.J. Greatbatch, and P. Fardy. 1994. Advection diffusion modelling of capelin larvae in Conception Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 51: 1297–1307.

deYoung, B., R.J. Greatbatch, and K.B. Forward. 1993*a*. A diagnostic circulation model with application to Conception Bay, Newfoundland. J. Phys. Oceanogr. 23: 2617–2635.

deYoung, B., T. Otterson, and R.J. Greatbatch. 1993*b*. The local and non-local response of Conception Bay to wind forcing. J. Phys. Oceanogr. 23: 2636–2649.

deYoung, B., and B. Sanderson. 1995. The circulation and hydrography of Conception Bay, Newfoundland. Atmos. Ocean. 33: 135–162.

Fortier, L., and W.C. Leggett, 1985. A drift study of larval fish survival. Mar. Ecol. Prog. Ser. 25: 245–257.

Frank, K.T., and W.C. Leggett. 1982. Coastal water mass replacement: its effect on zooplankton dynamics and the predator–prey complex associated with larval capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. 39: 991–1003.

Frank, K.T., J. W. Loder, J.E. Carscadden, W.C. Leggett, and C.T. Taggart. 1992. Larval flatfish distributions and drift on the southern Grand Banks. Can. J. Fish. Aquat. Sci. 49: 467–483.

Greatbatch, R.J., and T. Otterson. 1991. On the formulation of open boundary conditions at the mouth of a bay. J. Geophys. Res. 96: 18431–18445.

Harden Jones, F.R. 1968. Fish migration. Edward Arnold, London. 325 p.

Heath, M., and P. MacLachlan. 1987. Dispersion and mortality of yolk-sac herring (*Clupea harengus* L.) larvae from a spawning ground to the west of the Outer Hebrides. J. Plankton Res. 9: 613–630.

Hewitt, R.P., and R.D. Methot. 1982. Distribution and mortality of northern anchovy larvae in 1978 and 1979. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 226–245.

Horne, J.K., and D.C. Schneider. 1994. Analysis of scale-dependent processes with dimensionless ratios. Oikos, 70: 201–211.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. Ser. 2: 17–29.

Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U.S. 87: 471–496.

Iles, T.D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science (Washington, D.C.), 215: 627–633.

Kim, S., and B. Bang. 1990. Oceanic dispersion of larval fish and its implication for mortality estimates: case study of walleye pollock larvae in Shelikof Strait, Alaska. Fish. Bull. U.S. 88: 303–311.

Laprise, R., and P. Pepin. 1995. Factors influencing the spatio-temporal occurrence of fish eggs and larvae in a northern, physically-dynamic coastal environment. Mar. Ecol. Prog. Ser. 122: 73–92.

Large, W.G., and S. Pond. 1981. Open ocean momentum flux measurements in moderate to strong winds. J. Phys. Oceanogr. 11: 324–336.

MacDonald, P.D.M., and J.T. Pitcher. 1979. Age-groups from size–frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36: 987–1001.

McGurk, M.D. 1989. Advection, diffusion, and mortality of Pacific herring larvae *Clupea harengus pallasi*, in Bamfield Inlet, British Columbia. Mar. Ecol. Prog. Ser. 51: 1–18.

Morse, W.W. 1989. Catchability, growth, and mortality of larval fish. Fish. Bull. U.S. 87: 417–446.

Munk, P., V. Christensen, and H. Paulsen. 1986. Studies of a larval herring (*Clupea harengus*) patch in the Buchan area. II. Growth, mortality, and drift of larvae. Dana Rep. Carlsberg Found. 6: 11–24.

Pepin, P. 1991. The effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48: 503–518.

Pepin, P. 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of a multispecies study with an empirical review. Can. J. Fish. Aquat. Sci. 50: 2166–2174.

Power, J.H. 1986. A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California current. Fish. Bull. U.S. 84: 585–603.

Reed R.K., L.S. Incze, and J.D. Shumacher. 1989. Estimation of the effects of flow on dispersion of larval pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska, p. 239–246. *In* R.J. Beamish and G.A. MacFarlane [ed.] Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Aquat. Sci. 108.

Shelton, P.A., and L. Hutchings. 1982. Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. J. Cons. Cons. Int. Explor. Mer, 40: 185–198.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, Wash. 251 p.

Taggart, C.T., and K.T. Frank. 1990. Perspectives on larval fish ecology and recruitment processes: probing the scales of relationships, p. 151–164. *In* K. Sherman, L.M. Alexander, and B.D. Gold [ed.] Large marine ecosystems: patterns, processes, and yields. American Association for the Advancement of Science, Washington, D.C.

Taggart, C.T., and W.C. Leggett. 1987. Short-term mortality in post-emergent capelin *Mallotus villosus*. I. Analysis of multiple in situ estimates. Mar. Ecol. Prog. Ser. 41: 205–217.

Talbot, J.W. 1977. The dispersal of plaice eggs and larvae in the Southern Bight of the North Sea. J. Cons. Cons. Int. Explor. Mer, 37: 221–248.

van Guelpen, L., D.F. Markle, and D.J. Duggan. 1982. An evaluation of accuracy, precision, and speed of several subsampling techniques. J. Cons. Cons. Int. Explor. Mer, 40: 220–230.

Morphology and microhabitat use in stream fish

Brian M. Wood and Mark B. Bain

Abstract: Microhabitat use and body morphology were compared among 15 warmwater stream fishes from the Alabama River (Alabama, U.S.A.) watershed. Morphological variation among separate populations of a species was detected in 14 of the 15 species, indicating that populations should be separated in analyses among species. Comparison of morphological variation between microhabitat generalist and specialist species suggested that all species may vary in morphology relative to their environment. Regression analysis showed that within two families, Cyprinidae and Percidae, morphology was related to specific microhabitat variables. In the Centrarchidae, morphology was not related to any microhabitat variables. Morphological differences among the species occurred along gradients that were similar to gradients of habitat utilization, indicating that within a family, species widely separated in microhabitat use were morphologically different and species using similar microhabitats were similar in morphology. Our results suggest that patterns of morphological variation correspond to properties of the available habitat for warmwater stream fish species.

Résumé : Nous avons comparé l'utilisation des microhabitats et la morphologie corporelle chez 15 poissons d'eaux chaudes provenant du bassin de la rivière Alabama (Alabama, États-Unis). Nous avons repéré une variation morphologique entre des populations séparées d'une même espèce chez 14 des 15 espèces, ce qui indique qu'il faudrait tenir compte des diverses populations dans les analyses portant sur les espèces. La comparaison de la variation morphologique entre les espèces généralistes et spécialistes sur le plan des microhabitats indique que, chez toutes les espèces, la morphologie semble varier en fonction de l'environnement. L'analyse de régression a montré que dans deux familles, les Cyprinidés et les Percidés, la morphologie était liée à des variables spécifiques aux microhabitats. Par contre, chez les Centrarchidés, la morphologie n'était liée à aucune telle variable. Les différences morphologiques entre les espèces apparaissaient selon des gradients qui étaient similaires aux gradients de l'utilisation de l'habitat, ce qui permet de penser que, dans une même famille, les espèces nettement séparées quant à l'utilisation des microhabitats étaient morphologiquement différentes, tandis que les espèces qui utilisaient des microhabitats similaires présentaient des ressemblances morphologiques. Nos résultats indiquent que les profils de variation morphologique correspondent aux propriétés de l'habitat dont disposent les espèces de poissons des eaux chaudes.

[Traduit par la Rédaction]

Introduction

The morphology of fish is regularly interpreted as a set of physical attributes linked to the use of habitat and food resources. Morphological investigations based upon this relationship include the function of characters (Keast and Webb 1966), community structure (Gatz 1979*a*), niche partitioning among species (Douglas 1987), distinctions among similar species (Baumgartner et al. 1988), and discrimination among separate populations (Shepherd 1991). Central to most of these studies is the assumption that morphology and ecology are directly related (Gatz 1979*a*; Felley 1984; Wimberger 1992). However, direct tests of this assumption are limited, and the generality of this assumption is not known.

When morphology and resource use have been investigated, morphometric measurements were typically limited to select body structures such as fins (e.g., Gatz 1979*b*;

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Felley 1984; Page and Swofford 1984) with poor or no ability to quantify body shape (Winans 1984). These measurements tended to concentrate on specific regions of the body, such as the head and caudal peduncle, causing analyses to be biased towards specific body regions (Winans 1984). More recently, comprehensive measurement of body shape has been refined (truss method of Strauss and Bookstein (1982)) and these data have been highly effective for differentiating both species and populations (Winans 1984; Roby et al. 1991; Wimberger 1992). In addition, truss data provide even areal coverage of the entire form of the fish (Humphries et al. 1981; Strauss and Bookstein 1982; Bookstein et al. 1985). Because truss data may better elucidate differences among fishes, relations between morphology and habitat should be better assessed using truss data than conventional data sets.

Before interspecific patterns in morphology can be interpreted, the extent of intraspecific morphological variation must be evaluated (Wiens and Rotenberry 1980). Substantial intraspecific variation in morphology has been documented for many fishes. Intraspecific morphological variation has been used to separate stocks of fishes (e.g., Shepherd 1991), explain intraspecific patterns in microhabitat use (e.g., Ehlinger 1990), document the influence of rearing conditions on a single brood of fish (Swain et al. 1991), and explain mechanisms of defense against predators (Brönmark and Miner 1992). The substantial plasticity of fishes suggests that intraspecific differences in morphology may influence comparisons of morphology among species. Therefore, interspecific morphological differences may be secondary to intraspecific differences at the microhabitat level.

Fish communities have often been shown to be organized primarily on the basis of habitat (Werner and Hall 1976; Werner et al. 1977; Schlosser and Toth 1984), and morphological investigations have indicated a relationship between habitat use and morphology (Keast and Webb 1966; Gatz 1979*b*; Felley 1984; Page and Swofford 1984). Habitat use by a species is generally consistent over the range of a species, indicating that many species found in small streams are habitat specialists (Gorman and Karr 1978). Although this generalization may hold for large habitat scales, microhabitat use by stream fishes often varies among individuals of a species (Moyle and Baltz 1985). Consequently, species may be classified as either microhabitat generalists (individuals differ in microhabitat use and use a wide range of available habitats) or specialists (individuals use specific and similar microhabitats). The link morphology may have with microhabitat use has received little attention, probably because few investigators of morphology have been able to obtain suitable data on microhabitat use.

In this paper, we use morphology to describe variation in microhabitat use of fish species found in warmwater streams. The specific objectives of this study were to (*i*) identify the extent of intraspecific morphological variation from collections in streams differing in habitat availability, (*ii*) identify variation in morphology and microhabitat use among species of stream fish, and (*iii*) relate variation in morphology to microhabitat use.

Materials and methods

Fish were collected from nine study sites on six streams located within the Alabama River watershed in Alabama (Fig. 1). Streams chosen for study included a United States Geological Survey streamflow gage, were unregulated, and had similar mean annual flows (Table 1). Water chemistry data from each stream indicated low conductivity (50–150 μmhos/cm; 1 mho = 1 S), low alkalinity (5–50 mg/L $CaCO_3$), and neutral to slightly acidic pH (6–7.5). Mean summer water temperatures ranged from 24 to 27°C across the six streams.

There were large differences among the six study streams in physical structure and flow regime (Table 1). Physical structure ranged from rocky, high-gradient streams with a stable, unchanging channel (e.g., Little River) to sandy, low-gradient streams with a shifting channel (e.g., Uphapee Creek). Flow regime among streams varied from highly unstable (e.g., Little River) with relatively great differences among peak, base, and mean flows to highly stable (e.g., Terrapin Creek) with relatively minor variations in flow statistics.

To obtain fish samples in discrete microhabitats, we used prepositioned area electrofishers (Bain et al. 1985). Electrofishers were located along four or six fixed transects selected to include common instream habitats at each study area. The electrofishers were placed along each transect to sample both midstream and margin areas. For midstream samples, electrofishers were placed at one third and two thirds of the transect width; stream width was measured from bank to bank perpendicular to the greatest amount of stream flow. Stream margins were sampled with one electrofisher with its outside edge directly at the water's edge and one electrofisher located on the opposite shore approximately 1 m from the water's edge. All sampling was done in May through September, during baseflow or near-baseflow conditions.

Fish were collected by electrifying the prepositioned area electrofishers approximately 30 min after placement. A 750-W AC generator and a variable voltage (maximum of approximately 900 V) transformer were used to power the electrofishers for approximately 20–30 s. The electrofishers measured 1.0 × 2.0 m and only sampled fish located between the electrodes. A 3.0 × 1.2 m seine with 3.2-mm mesh was placed immediately downstream of the electrofisher after power was activated to capture stunned fish, and then the seine was passed over the sample area. The substrate within the electrofisher was also disrupted by kicking to dislodge benthic fishes. Dip nets were used to capture fish in areas where the current would not sweep stunned fish into the seine. Fish were anesthetized with tricane methanosulfate (MS-222) and then placed into 10% Formalin. Approximately 1 week later the fish were transferred to a 50% isopropyl alcohol solution for preservation.

To quantify microhabitat conditions at each electrofisher location, a standardized sampling method was developed. Water depth, substrate type, and water velocity were recorded at each corner of the electrofisher and averaged for statistical analysis. A graduated wading rod was used to determine water depth. Current velocity was measured at

0.6 times the water depth with a Marsh–McBirney electronic current meter. Substrate type was categorized as clay (<0.06 mm), silt (0.06–0.1 mm), sand (0.11–1 mm), gravel (1.1–60 mm), cobble (60.1–150 mm), boulder (>150 mm), or bedrock (including hard clay bottoms). Cover was recorded as the number of objects with a diameter greater than 7 mm lying across the grid's perimeter.

Morphological measurements

Specimens for morphometric measurements were obtained from the preserved fish collections. Species with large numbers of individuals in more than one stream were selected for study. As a result, 15 species from three different families were selected (see Appendix). An attempt was made to measure 30 individuals at each site; however, the lack of suitable specimens reduced sample sizes at many sites. Individuals measured were taken randomly from the pool of suitable specimens at each site. At sites where collections were made in both 1989 and 1990, specimens from both years were combined. Differences in morphology between years were not tested because when specimens were combined, specimens from 1990 made up at least 80% of the sample. Overall, 1554 fish were measured.

Fish were measured and archived using the truss method of Strauss and Bookstein (1982) and the digitizing technique of Winans (1984). Ten identifiable and distinct landmarks were chosen to structure the truss system, resulting in a total of 21 morphometric measurements (Fig. 2). Each specimen was placed on water-resistant paper and landmark locations were recorded with a pin. Fish total length (measured with dial calipers), weight (measured with an electronic scale), and identification number were recorded beside the pinned form of each fish. The pin holes were then digitized as X-Y coordinates into a spreadsheet program where morphometric distances were calculated by computer using the Pythagorean theorem.

The precision of this approach was calculated using one species from each of the three families studied: orangefin shiner, bluegill, and greenbreast darter. Twenty specimens of each species were measured and digitized independently three times. Using a one-way analysis of variance, variation was separated into among and within groups. Repeatability for each measurement was calculated as the ratio of the among-group variation to the total variation (Falconer 1981; Baumgartner et al. 1988). Measurement repeatability ranged from 0.968 to 0.999, showing that the error of each measurement was very low.

Statistical analysis

Microhabitat data were standardized and morphological data were transformed prior to analysis. Habitat variables for each stream were standardized to account for flow regime and channel form differences among the different study streams. Using the mean (of the four measurements for each habitat variable) habitat measurements taken from the electrofishers, a grand mean and standard deviation for each habitat variable were calculated for all individuals of a species collected at each site. The mean habitat measurements for the electrofisher where each specimen was collected were then subtracted from the grand mean and divided by the standard deviation. The result was a new score for each habitat variable for each individual. The standardization scaled each stream's habitat conditions similarly: extremes in habitat conditions were given the highest values (both positive and negative) and the midrange conditions were given the lowest values (near zero). Morphological data were transformed using logarithms (base 10) before analysis because the transformation preserves allometries and produces scaling-independent covariances (Bookstein et al. 1985; Baumgartner et al. 1988). Analyses were performed using two statistics packages (Data Desk® 3.0 1989 and Systat 5.1 1991).

Multivariate analysis of covariance was used to test for differences in morphology within and among species. Multivariate analysis of covariance, prior to testing for significant differences in population centroids, uses a covariate to adjust the set of dependent variables (Pimentel 1979). Total length was used as a covariate in the multivariate analysis of covariance to eliminate the confounding effect of size from the tests. A significant Wilks' lambda statistic indicated that significant shape differences existed. Because of the large morphological differences among the three family groups, separate analyses were conducted for each group.

Principal components analysis was used to illustrate microhabitat use and morphological differences among the species. Principal components from the standardized microhabitat features were computed using the correlation matrix,

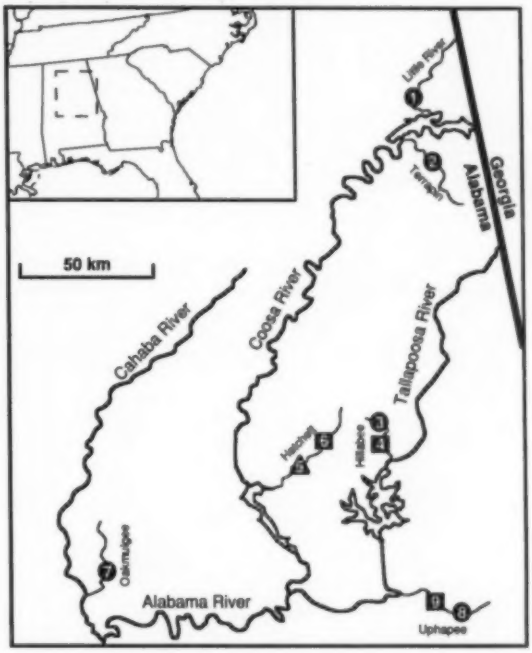


Fig. 1. Location of study sites within the Alabama River basin. Study sites denoted by circles indicate sites sampled in both 1989 and 1990, triangles indicate sites sampled only in 1989, and squares indicate sites sampled only in 1990. Study site numbers are denoted under the column study site code in Table 1.

Table 1. Stream flow data and physical characteristics of each study site.

		USGS gage data					Field data	
Stream	Study site code	Drainage area (km^2)	Peak flow (m^3/s)	Base flow (m^3/s)	Mean annual discharge (m^3/s)	CV (%)	Site gradient (cm/m)	Common substrates[a]
Little River	LRN (1)	515	150.7	0.1	5.4	132	0.26	Cob, Grvl, Snd
Terrapin Creek	TER (2)	635	25.9	1.7	7.1	30	0.01	Cob, Grvl
Hillabee Creek	HIL1 (3)	492	57.2	0.3	3.7	144	0.01	Grvl, Snd, Cob
	HIL2 (4)						1.12	Grvl, Cob, Snd, Bld
Hatchett Creek	HAT1 (5)	681	66.3	0.6	3.6	50	0.01	Grvl, Snd, Cob, Bld
	HAT2 (6)						1.13	Cob, Bld, Grvl, Bed
Oakmulgee Creek	OAK (7)	570	15.5	0.5	2.8	72	0.01	Grvl, Snd
Uphapee Creek	UPH1 (8)	862	212.4	0.4	8.2	77	0.01	Grvl, Snd, Cly, Slt
	UPH2 (9)						0.01	Snd, Grvl, Slt

Note: United States Geological Survey (USGS) data were taken from a representative and comparable set of records (water year 1986) for gages located on each study stream. Field data were based on habitat surveys conducted during base-flow conditions. Peak flow indicates the highest daily discharge measured during the water year while base flow was the typical mean daily discharge during the dry period (May–November). The coefficient of variation (CV) for mean annual discharge was calculated from the daily discharge data. Site gradient was calculated as the elevation change from the upstream to the downstream end of study site divided by site length.

[a]Bed, bedrock; Bld, boulder; Cly, Clay; Cob, cobble; Grvl, gravel; Slt, silt; Snd, sand.

because the habitat variables were measured on different scales and the standardization of variation that occurs with the correlation matrix was required (Pimentel 1979). The important habitat components (eigenvalues > 1.0) were then used to plot species locations in multivariate habitat space. The variance–covariance matrix was used to obtain principal components from the morphological data. The variance–covariance matrix measures absolute variation and was used because each variable was measured on an equal scale (Pimentel 1979). Components with eigenvalues > 0.7 were considered as important components because they provided ecologically interpretable information (Matthews 1985). The shear procedure described by Humphries et al. (1981) and Bookstein et al. (1985) was utilized to ensure that the morphology components were not confounded with size information. The shear did not produce a difference in coefficients, and therefore the morphology components were assumed not to be confounded with size variation.

Multivariate analysis of variance was used to evaluate association between habitat attributes and the presence of a species. For each species, the hypothesis that habitat composition was not different among samples with and without a species was tested. Initially a complete model with all habitat variables was tested and variables were eliminated on the basis of canonical loadings and changes in the F statistic for the model. Different models were tested until the simplest model (less variables) was found that best identified species absence or presence. Models including only one variable were reported as an analysis of variance model, while models including more than one variable were reported as a multivariate analysis of variance model.

Regression analysis was utilized to develop relationships between morphology and microhabitat use. Morphological variables created in principal components analysis for each family group were regressed against the variables from the principal components analysis for the microhabitat data. The result was three separate regression analyses that determined if relationships were present between morphology and microhabitat use for each family.

Multivariate statistical analyses include two assumptions that must be met for the analyses to be valid. These assumptions are that the dependent variables are multinormally distributed and that the within-group dispersion matrices are equal across the treatment groups (Hair et al. 1984). Although these assumptions were not directly tested in this study, they were accepted as valid because similar studies have confirmed that morphological data meet the assumptions. For example, Pimentel (1979) and Misra and Ni (1983) state that multivariate normality is closely approximated by the logarithms of morphometric measurements taken on continuous variables. Baumgartner et al. (1988) tested the normality of morphometric variables and principal component scores and found that 84% of the variables had no departure from normality and the other 16% were only slightly non-normal. The homogeneity of dispersion matrices was tested by Taylor and McPhail (1985). Although they found differences among matrices, they felt that their analyses were not compromised because of their large sample sizes of 25. Because our sample sizes were equally large and logarithmically transformed, we feel that the assumptions of our multivariate analyses were adequately met.

Results

Significant intraspecific morphological variation was found among stream populations in 14 of 15 species using multivariate analysis of covariance ($P < 0.01$, Table 2). In the Cyprinidae and Percidae, each species varied in morphology among populations. In the Centrarchidae, one species,

bluegill, did not vary in morphology among stream populations. The observed variation in morphology among populations indicated that each study stream has morphologically unique fish within a species, and therefore populations should not be pooled for the study of morphology–habitat relations.

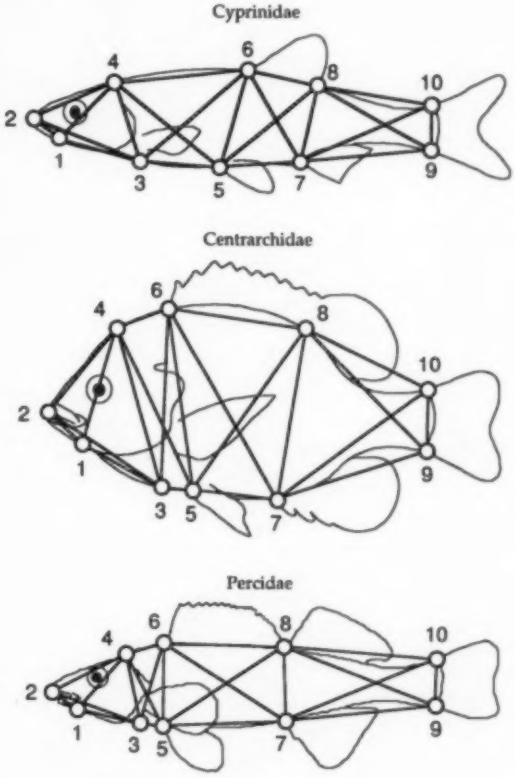
Multivariate analysis of covariance indicated that within each family, species differed in morphology ($P < 0.01$). Principal components analysis illustrated morphological differences within each family. In each analysis, the first component was considered a size component because it was comprised of coefficients with relatively equal and similar values (Humphries et al. 1981; Winans 1984; Bookstein et al. 1985). Subsequent bipolar components were characterized as shape components. These bipolar shape components discriminated species within each family. Shape components from each of the family-group principal component analyses were not correlated with either fish total length or body weight ($P > 0.05$). Pearson correlation coefficients between shape principal components and fish total length were very small ($r \leq 0.09$). The lack of correlation between the shape components and total length and weight indicates that these analyses were measuring actual shape differences among the species and not simply differences in length or weight.

The pattern of morphometric variation among cyprinids was best illustrated by the second principal component of cyprinid morphology. The first component (92% of the total variation) largely explained size variation. The second component (2% of the total variation) separated the species along a morphological gradient (Fig. 3). Five truss measurements largely explained the variation among the species: mouth shape and the relative positions of the dorsal and anal fins. Positive and negative principal component loadings defined a gradient in shape with extremes marked by species with smaller, subterminal mouths with a relatively large distance between the origins of the dorsal and anal fins (e.g., largescale stoneroller), to species with larger, superior mouths and a small distance between the origins of the dorsal and anal fins (e.g., silverstripe shiner).

The pattern of variation among centrarchids was best illustrated by using one shape component (2% of total variation). This component poorly discriminated the three species (Fig. 4), which was expected given the mixed significance results in Table 2. Ninety-five percent confidence intervals for the mean of the shape component for each species had a high amount of overlap, indicating little variation in morphological scores among the three species. Principal component loadings defined variation in two different truss measurements: mouth length and distance between the pectoral fin origin and pelvic fin origin. However, these measurements were not sufficient to separate the three species.

Three components were identified in the principal components analysis for the four darter species. The two shape components (each 3% of the total variation) illustrated the differences among the species (Fig. 5). The second component primarily separated one species from the other three, while the third component almost completely separated the four species. Principal component loadings on the second component (first shape component) contrasted two

Fig. 2. Locations of the 10 truss landmarks on specimens from each family studied. Landmarks are denoted by circles along the outline of specimen drawings. For landmarks not on the outside of body form, points were made at the closest point to the body on a line perpendicular to the horizontal axis of the specimen (Winans 1984). Landmarks refer to (1) most posterior point of maxillary, (2) most anterior point of jaw, (3) origin of pectoral fin, (4) most posterior part of neurocranium, (5) origin of pelvic fin, (6) origin of dorsal fin (or spinous dorsal fin), (7) origin of anal fin, (8) insertion of dorsal fin (or beginning of soft dorsal or origin of soft dorsal fin), (9) anterior attachment of ventral membrane from caudal fin, and (10) anterior attachment of dorsal membrane from caudal fin. Specimen sketches taken from Robison and Buchanan (1988).



length truss measurements and four body-depth truss measurements (Fig. 5), indicating body slenderness. Five truss measurements largely explained variation in shape for the third component: compression of the body about the pectoral and pelvic fins and a concurrent elongation of the body (Fig. 5).

Multivariate analysis of variance identified microhabitat variables that predicted the presence of a species (Table 3). In general, most species showed a significant association with some microhabitat attribute at each study site, although

Table 2. Probability values from tests of intraspecific morphological variation among study sites using univariate and multivariate analysis of covariance of morphometric variables.

	Cyprinidae								Centrarchidae			Percidae			
Measurement	LSS	ALS	BTS	STS	PTS	OFS	SLS	MIS	RED	BLU	LON	GBD	SPD	BBD	BZD
1–2	0.21	0.24	0.02	0.04	0.01	0.02	0.02	0.01	0.21	0.97	0.04	0.09	0.08	0.30	0.84
2–4	0.01[a]	0.84	0.01[a]	0.01[a]	0.59	0.15	0.12	0.02	0.24	0.72	0.72	0.01[a]	0.32	0.02	0.17
1–3	0.01	0.02	0.01[a]	0.18	0.02	0.01	0.01[a]	0.01[a]	0.49	0.42	0.16	0.01[a]	0.33	0.01[a]	0.77
2–3	0.01	0.16	0.01[a]	0.01	0.58	0.02	0.01[a]	0.04	0.43	0.59	0.63	0.01[a]	0.18	0.01	0.01[a]
1–4	0.01	0.15	0.01[a]	0.01	0.13	0.88	0.01[a]	0.01[a]	0.45	0.74	0.22	0.01[a]	0.95	0.01	0.07
3–4	0.05	0.11	0.01[a]	0.01[a]	0.28	0.03	0.01[a]	0.74	0.59	0.89	0.03	0.14	0.11	0.50	0.30
4–6	0.89	0.02	0.01[a]	0.01	0.72	0.40	0.03	0.37	0.43	0.97	0.19	0.56	0.83	0.26	0.78
3–5	0.01	0.66	0.05	0.21	0.49	0.15	0.01	0.01[a]	0.01	0.89	0.21	0.01[a]	0.01[a]	0.01[a]	0.01[a]
4–5	0.08	0.23	0.01[a]	0.01[a]	0.89	0.01[a]	0.01[a]	0.22	0.53	0.99	0.17	0.26	0.07	0.03	0.01
3–6	0.18	0.87	0.01[a]	0.01[a]	0.34	0.03	0.63	0.01	0.14	0.76	0.01[a]	0.02	0.24	0.02	0.06
5–6	0.03	0.01[a]	0.01[a]	0.01[a]	0.67	0.02	0.09	0.01[a]	0.10	0.91	0.01	0.05	0.06	0.01[a]	0.01
6–8	0.01[a]	0.26	0.20	0.01[a]	0.92	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.76	0.22	0.25	0.10	0.35	0.57
5–7	0.19	0.36	0.13	0.99	0.45	0.13	0.01[a]	0.89	0.67	0.91	0.03	0.09	0.14	0.21	0.05
6–7	0.02	0.02	0.05	0.18	0.34	0.01	0.01	0.07	0.03	0.40	0.25	0.49	0.43	0.53	0.15
5–8	0.17	0.11	0.01[a]	0.01[a]	0.82	0.01	0.01	0.01[a]	0.02	0.71	0.03	0.17	0.03	0.06	0.51
7–8	0.11	0.01[a]	0.01[a]	0.01[a]	0.85	0.10	0.85	0.15	0.01[a]	0.83	0.01	0.01	0.03	0.01[a]	0.08
8–10	0.01[a]	0.01	0.16	0.21	0.09	0.91	0.01	0.01[a]	0.10	0.07	0.27	0.01	0.20	0.01	0.04
7–9	0.18	0.31	0.63	0.01[a]	0.01[a]	0.35	0.77	0.26	0.17	0.08	0.23	0.03	0.03	0.01[a]	0.05
8–9	0.01[a]	0.03	0.12	0.05	0.02	0.57	0.02	0.01[a]	0.55	0.10	0.05	0.01[a]	0.35	0.01[a]	0.03
7–10	0.26	0.35	0.11	0.01[a]	0.01	0.01	0.08	0.63	0.36	0.30	0.40	0.03	0.02	0.01	0.01
9–10	0.89	0.12	0.01[a]	0.01[a]	0.11	0.01[a]	0.06	0.52	0.26	0.60	0.36	0.07	0.43	0.13	0.01[a]
Multivariate	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.01[a]	0.66	0.01	0.01[a]	0.01[a]	0.01[a]	0.01[a]

Note: Body length was used as the covariate. Measurements are shown in Fig. 2. Species cores are in the Appendix. Probability values of 0.01 indicate a value less than or equal to 0.01.

[a]The variable would be significant at the species-wide sequential Bonferroni (Rice 1989) probability value of 0.00227.

no significant associations occurred in 10 analyses out of 55 species–site combinations. The significant associations with habitat suggested that species used specific microhabitats at each study site. However, specific microhabitat use did vary among study streams, reflecting intraspecific variation in this behavior.

Principal components analysis characterized general microhabitat use by each species. Variation in the microhabitat data was represented by two components comprising approximately 60% of the total variation in microhabitat conditions across all sites. The first habitat component was dominated by two microhabitat variables: current velocity and substrate type. The first component defined a gradient from fast water with coarse substrate to slow water with fine substrate, whereas the second component contrasted water depth and amount of cover (Fig. 6). The mean position (centroid) of each species was plotted within this microhabitat space. Species centroids illustrated patterns of microhabitat use among the species and families (Fig. 6). The cyprinid species were distributed in a gradient from shallow, high-cover microhabitats with medium current speeds and substrate sizes to deep microhabitats with less cover. However, they also showed some differences in use of available current speeds and substrate types. In contrast, the three sunfish species used similar microhabitats. Centroid locations for all three were concentrated in areas of slow current velocity and fine substrate with moderate depth and cover. The four darter species were distributed in a gradient from fast current and coarse substrates to slower current speeds with finer substrates. These patterns reflected the general use of available microhabitat conditions by each family, although they obscure intraspecific morphological variation.

For Cyprinidae and Percidae, regression analysis indicated significant ($P < 0.05$) relationships between variables defined in principal components analyses of morphology and the standardized microhabitat variables from the analysis of habitat components. Results from regression analyses were similar if species were combined over all sites or if sites were separated. However, sites were separated because most species exhibited intraspecific variation among the populations. The second habitat component, contrasting water depth and the amount of cover, was inversely related to cyprinid morphology (Fig. 7). In contrast, both components from the percid analysis were significantly related to the first habitat component, a gradient from fast current speeds and coarse substrates to slow current speeds and fine substrates (Fig. 8). However, the third component was more strongly correlated to current velocity than was the second component. Regression analysis did not show a significant relationship between sunfish morphology and microhabitat use.

Table 3. Attributes of habitat associated with presence of a species as determined by multivariate and univariate analysis of variance.

	Study stream								
	LRN	TER	HIL1	HIL2	HAT1	HAT2	OAK	UPH1	UPH2
Cyprinidae									
Largescale stoneroller	SH,FA	SH,FA	SH,CO	ns	—	CO	—	—	—
Alabama shiner	SH,CO	—	CO,SH	SH	—	SH,FI	—	—	—
Blacktail shiner	—	—	SL,FI	—	—	—	ns	CP	FA,CO
Striped shiner	—	—	ns	—	—	—	SH,SL	—	—
Pretty shiner	—	—	DP	—	—	—	ns	SL,DP	—
Orangefin shiner	—	—	—	—	—	—	SH,SL	SH	SH
Silverstripe shiner	ns	—	ns	—	FA	—	—	—	—
Mimic shiner	—	—	—	—	—	FA	SH,CP	FI	—
Centrarchidae									
Redbreast sunfish	SL,SH,CP	SL,FI	SL,FI	—	—	—	—	—	—
Bluegill	SL	SL,DP	—	—	—	—	—	—	—
Longear sunfish	—	FI,SL	—	—	—	—	CP,SL	CP,SL	—
Percidae									
Greenbreast darter	SH,CO,FA	ns	FA,CO,SH	FA,SH	—	FA,SH	—	SH,FA,CO	—
Speckled darter	SL	—	SH,SL	ns	—	—	SH,CO	—	—
Blackbanded darter	SH,CO	FA,SH	—	—	—	ns	SH,CP	FA,CP	FA,CP
Bronze darter	SH,CO	—	SH,CO	ns	—	NS,CO	—	—	—

Note: Abbreviations for habitat attributes are as follows: SH, shallow; DP, deep; FI, fine substrate; CO, coarse substrate; SL, slow velocity; FA, fast velocity; CP, cover present; NC, no cover; ns, no attributes significant. Dashes indicate that a species was not present. Habitat attributes are listed in order of importance. Study stream abbreviations are denoted in Table 1.

Discussion

Intraspecific morphological differences among separate populations were observed in our study and in previous studies on many different fish species (Berg 1979; Gatz 1979*a*; Ihssen et al. 1981; Riddell and Leggett 1981; Winans 1984; Beacham 1985; Taylor and McPhail 1985; Layzer and Clady 1987; Matthews 1987; Ehlinger 1990; Karakousis et al. 1991; Shepherd 1991; Swain et al. 1991). Many authors have noted that, within a species, morphological features are responsive to local habitat conditions. Swain et al. (1991) suggested that coho salmon (*Oncorhynchus kisutch*) have a phenotypic plasticity that allows them to adapt to their local environment. Riddell and Leggett (1981) hypothesized that morphological differences in juvenile Atlantic salmon (*Salmo salar*) were adaptive responses to long-term flow conditions. Similarly, Beacham (1985) concluded that morphometric variation in pink salmon (*Oncorhynchus gorbuscha*) reflected adaptation to local water velocity in spawning streams. Our data indicated morphometric differences among separate populations, including populations located within the same stream. Consequently, the populations should be separated when testing for relationships between morphology and habitat at the interspecific level.

Variation in morphology among populations did not appear to confound the analysis of morphology among species. Within a species, populations were relatively similar in morphology compared with other species, and populations grouped together when compared with populations of other species. Recently, Douglas and Matthews (1992) suggested that the phenotype of fishes acts as a constraint on the ecology of an individual, therefore limiting the ability of an individual to adapt to local conditions. Our data support and elucidate this conclusion. While individuals of a species may vary in morphology depending on attributes of their local environment, their morphology is restricted by the phylogenetic processes that made the species unique.

Multivariate analysis of variance indicated that 11 of the 15 species could be classified as microhabitat specialists because they used a statistically distinct subset of microhabitat conditions and they often used similar types of microhabitats in different streams. Four other species (blacktail shiner, striped shiner, silverstripe shiner, and mimic shiner) sometimes used a statistically distinct microhabitat, and the type of microhabitat differed among streams. However, these generalist species did not vary at a greater degree than did the specialists in the morphology–habitat relations analysis (Fig. 7). Therefore, although a microhabitat specialist may use very distinct microhabitats, they still have the ability to vary in morphology relative to their environment, an ability that generally would be given to a microhabitat generalist.

Cyprinid species have, in previous studies, been shown to partition habitat by stratifying the water column into

Fig. 3. Histogram of the distribution of the principal components scores from the Cyprinidae principal components analysis. Shaded areas indicate bars that include the 95% confidence intervals for the mean principal components score for each species. Sample sizes are denoted for each species. Highlighted landmark lines identify the measurements loading most heavily in the principal components analysis and indicate measurements separating the species. Measurements from one sketch are contrasted with measurements from the other sketch to define morphological differences among the species.

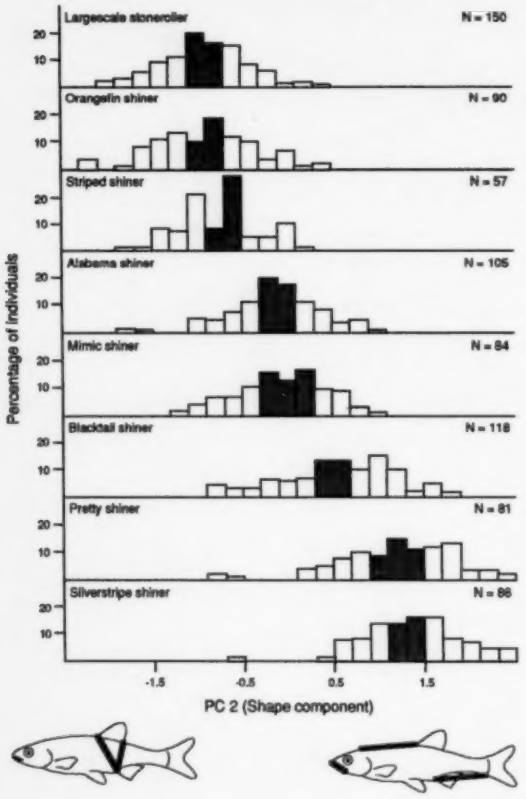
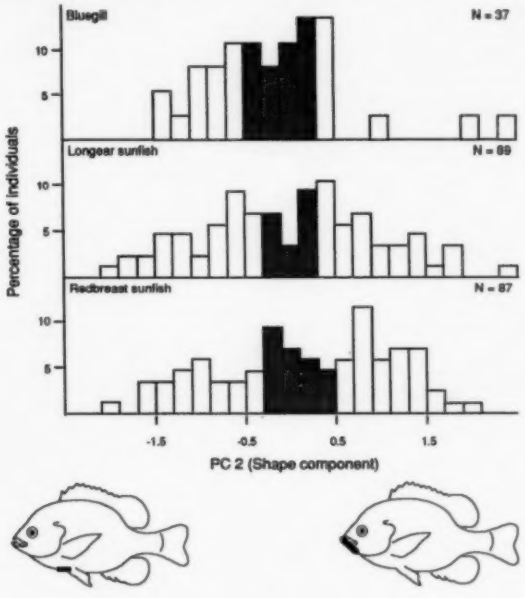


Fig. 4. Histogram of the distribution of the principal components scores from the Centrarchidae principal components analysis. Shaded areas indicate bars that include the 95% confidence intervals for the mean principal components score for each species. Sample sizes are denoted for each species. Highlighted landmark lines identify the measurements loading most heavily in the principal components analysis and indicate measurements separating the species. Measurements from one sketch are contrasted with measurements from the other sketch to define morphological differences among the species.



vertical zones (Gorman and Karr 1978; Douglas 1987). In addition, Gorman and Karr (1978) pointed out that habitat segregation might be based upon morphological adaptations, and Felley (1984) found significant correlations between specific morphological variables and water depth. In this study, cyprinids segregated the available range of habitat by the depth of water and presence of cover possibly owing to vertical separation of habitat. Five morphological measurements were important in associating cyprinid morphology and use of habitat. The divergence of these measurements, showing differentiation in mouth type and in the relative locations of the dorsal and anal fins among the species, suggests some adaptive advantages of morphology relative to the depth of water inhabited. Mouth types ranged from subterminal in the largescale stoneroller to superior in the pretty shiner and silverstripe shiner. Because these species were on opposite ends of the morphological and habitat spectrums, mouth type was assumed to indicate where a species obtained its food (Keast and Webb 1966; Aleev 1969; Gatz 1979*b*; Felley 1984). The positions of the dorsal and anal fins showed similar relationships. In shallow water forms, such as largescale stoneroller and Alabama shiner, the dorsal fin is completely anterior of the anal fin while in deeper water forms, such as pretty shiner and silverstripe shiner, the insertion of the dorsal fin is posterior to the origin of the anal fin. The positions of these fins indicate a change from maneuverability in shallow water forms, where the more anterior dorsal fin acts as a rudder, to stability in deeper water forms, where the more caudal dorsal fin acts as a stabilizer (Aleev 1969; Felley 1984). The species with intermediate forms, such as blacktail shiner, that used midrange water depths, generally had terminal mouths for foraging at midwater depths and moderately separated dorsal and anal fins that could be used both for stability and as a rudder.

Strong correlations between darter morphology and specific habitat variables indicated a strong relationship between habitat use and morphology (Page and Swofford 1984). Winn (1958) and Gorman and Karr (1978) noted that darters

Fig. 5. Histograms of the distributions of the principal components scores from the second and third components of the Percidae principal components analysis. Shaded areas indicate bars that include the 95% confidence intervals for the mean principal components score for each species. Sample sizes are denoted for each species. Highlighted landmark lines identify the measurements loading most heavily in the principal components analysis and indicate measurements separating the species. Measurements from one sketch are contrasted with measurements from the other sketch to define morphological differences among the species.

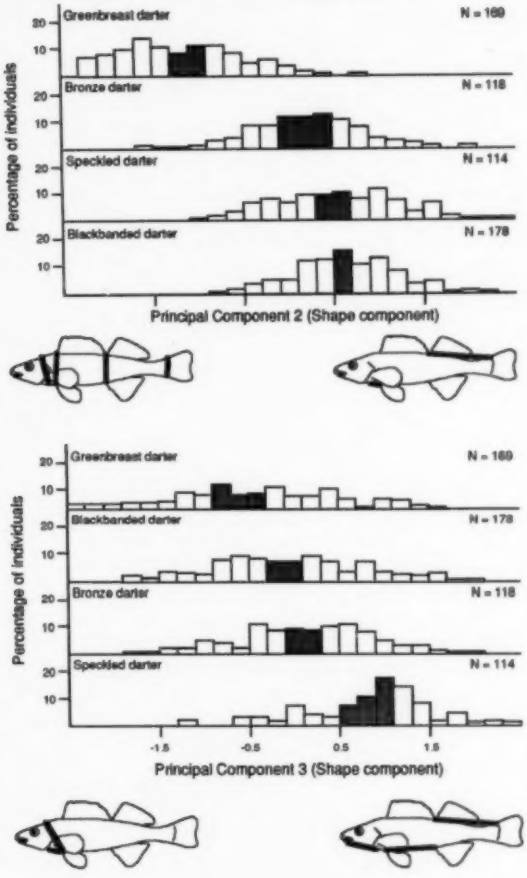
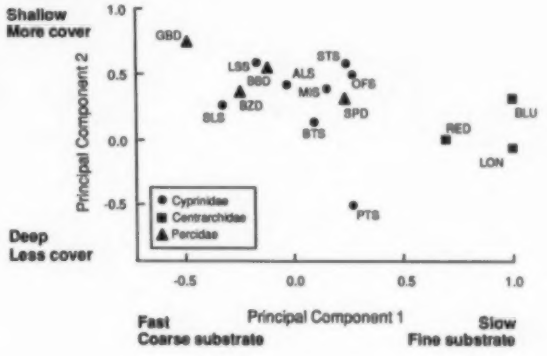


Fig. 6. Species centroid locations from principal components analysis on standardized microhabitat data from samples where fish were captured. Microhabitat attributes that characterize each component are shown along the axes. Species codes are defined in the Appendix.



subdivide riffles horizontally on the basis of current and substrate. Fisher and Pearson (1987) noted that four *Etheostoma* species found in riffles were segregated by current velocity, but not substrate. In our study, regression analysis related darter morphology to current velocity and substrate. Therefore, it appears that darter species horizontally segregate habitat by current velocity and substrate type, and, like the cyprinids, have morphologies related to their microhabitat use.

Two sets of morphological measurements separated the four species of darters and were related to current velocity. Because substrate type is highly dependent on current velocity, current velocity was assumed to be most important in influencing the selection of habitat by darters. The first set, a body slenderness component, contrasted body depth and body length. It was comprised of four depth and two length measurements that revealed a shift from short, compact species (greenbreast darter) to longer bodied, narrower species (blackbanded darter). This set of measurements was related to current velocities as shown by Page and Swofford (1984), who noted that darters found in swifter waters (riffles) have a deep body and deep caudal peduncles (greenbreast darter) while darters found in moderate-speed waters (runs) have more fusiform bodies and narrower caudal peduncles (speckled darter). The second set of measurements, denoting compression about the pectoral and pelvic fins and a lengthening of the body, was also related to current velocity. It not only denoted a gradient from short and compact to long and narrow, but also indicated a small change in distance between the pectoral and pelvic fins. In the greenbreast darter, a short-bodied darter, there was a greater distance between the two fins than in the speckled darter, a longer bodied darter. The more anterior position of the pectoral fin in the greenbreast darter could aid in maintaining position on the substrate by acting to push the darter down when the water flow hits the fin. Page and Swofford (1984) suggested that the current flowing against the pectoral fins of riffle-dwelling darters pushes down and helps the darter maintain its position. In contrast, the closer proximity of the pectoral and pelvic fins of the speckled darter, a slower water darter, would permit greater maneuverability and hence more movement.

Although the truss data set did not produce differences among the three sunfish species, many studies have documented variation in morphological characters among *Lepomis* species (Keast and Webb 1966; Gatz 1979*a*, 1979*b*; Douglas and Avise 1982; Mittelbach 1984; Kieffer and Colgan 1992). Two reasons may account for the lack of morphological differences among the sunfish species. First, one truss measurement, distance between the origins of

Fig. 7. Plot of regression analysis between cyprinid principal component 2 centroids and the standardized habitat principal component 2 centroids. Microhabitat attributes that characterize the component are shown along the horizontal axis.

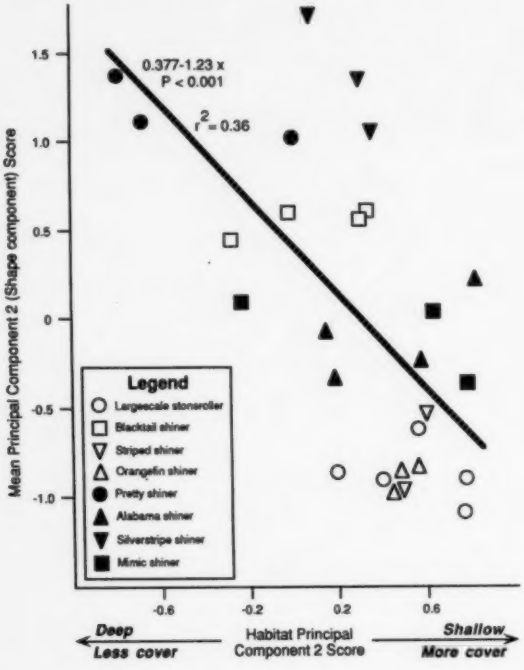
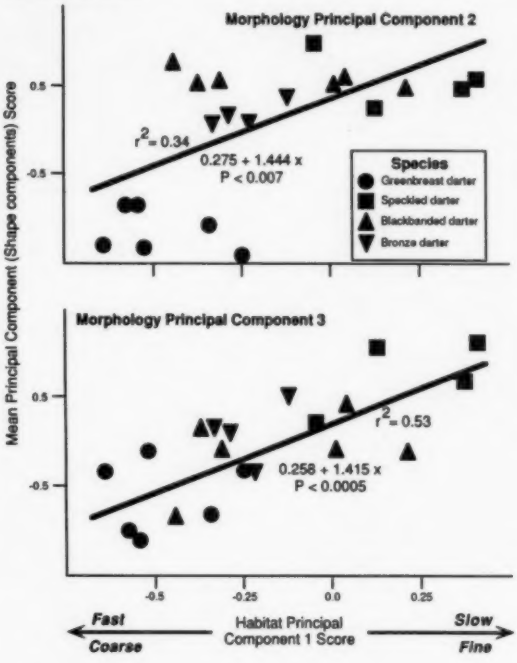


Fig. 8. Plots of regression analysis between percid principal component 2 and principal component 3 centroids and the standardized habitat principal component 1 centroids. Microhabitat attributes that characterize the component are shown along the horizontal axis.



the pectoral and pelvic fins, had a higher amount of measurement variation than the other 20 measurements. Because the body morphology of these three species appears to be very similar, a high degree of variation in one measurement could possibly conceal slight differences in morphology. Secondly, the truss measurements used in this study may not be sufficient to separate the three species. Douglas and Avise (1982) stated that, morphologically, the members of the Cyprinidae family were no more differentiated from one another than were the *Lepomis* species. However, Felley (1984) noted that morphological relationships pertinent for one species group may not be relevant to other species groups. Previous morphological studies separating sunfish have often used up to 50 morphological characters, including several fin, body, and internal measurements not incorporated within this study. We conclude that the truss system was not sufficient to separate the three species because characters used to separate the three species in other studies were not included in ours.

Although our approach to measuring morphology differed from that of previous studies using stream fish species, the conclusions we have drawn from the truss morphometric data are similar. Like Gatz (1979*b*), Felley (1984), and Wikramanayake (1990), we found that morphology can be predicted from microhabitat use and therefore support the assumption that morphology and ecology are related. Our results also indicate that although a species may vary in morphology among sites, the variation is not sufficient to confound interspecific morphometric analyses.

Morphological differences were greatest among species that differed most in microhabitat use. Species ranging greatly in use of microhabitat, such as the eight cyprinid species, were simultaneously highly separated in morphological space. In contrast, species in the same microhabitats, like the sunfish, showed little separation in morphology. This finding relates well to previous studies using different morphological measurements. Felley (1984) noted that cyprinid fin sizes and placements were indicative of preferred position in the water column. Page and Swofford (1984) reported that taxonomically distant darters occupying similar habitats resembled one another morphologically more than they resembled closely related (e.g., same genus) species. Overall, habitat is considered to be a primary factor in the organization of fish communities (Schoener 1974; Werner and Hall 1976; Werner et al. 1977; Bain et al. 1988), and our results indicate that patterns of morphological variation also correspond to the properties of available habitat for many species and populations.

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References

Aleev, Y.G. 1969. Function and gross morphology in fish. Israel Program for Scientific Translations, Jerusalem, Israel.

Bain, M.B., J.T. Finn, and H.E. Booke. 1985. A quantitative method for sampling riverine microhabitats by electrofishing. N. Am. J. Fish. Manage. 5: 489–493.

Bain, M.B., J.T. Finn, and H.E. Booke. 1988. Streamflow regulation and fish community structure. Ecology, 69: 382–392.

Baumgartner, J.V., M.A. Bell, and P.H. Weinberg. 1988. Body form differences between the Enos Lake species pair of threespine sticklebacks (*Gasterosteus aculeatus* complex). Can. J. Zool. 66: 467–474.

Beacham, T.D. 1985. Meristic and morphometric variation in pink salmon (*Oncorhynchus gorbuscha*) in southern British Columbia and Puget Sound. Can. J. Zool. 63: 366–372.

Berg, R.E. 1979. External morphology of the pink salmon, *Oncorhynchus gorbuscha*, introduced into Lake Superior. J. Fish. Res. Board Can. 36: 1283–1287.

Bookstein, F.L., B. Chernoff, R.L. Elder, J.M. Humphries, G.R. Smith, and R.E. Strauss. 1985. Morphometrics in evolutionary biology. Spec. Publ. Acad. Nat. Sci. Phila.

Brönmark, C., and J.G. Miner. 1992. Predator-induced phenotypical change in body morphology in crucian carp. Science (Washington, D.C.), 258: 1348–1350.

Douglas, M.E. 1987. An ecomorphological analysis of niche packing and niche dispersion in stream fish clades, p. 144–149. *In* W.J. Matthews and D.C. Heins [ed.] Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Okla.

Douglas, M.E., and J.C. Avise. 1982. Speciation rates and morphological divergence in fishes: tests of gradual versus rectangular modes of evolutionary change. Evolution, 36: 224–232.

Douglas, M.E., and W.J. Matthews. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos, 65: 213–224.

Ehlinger, T.J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. Ecology, 71: 886–896.

Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. Longman Group Limited, London, Great Britain.

Felley, J.D. 1984. Multivariate identification of morphological–environmental relationships within the Cyprinidae (Pisces). Copeia, 1984: 442–455.

Fisher, W.L., and W.D. Pearson. 1987. Patterns of resource utilization among four species of darters in three central Kentucky streams, p. 69–76. *In* W.J. Matthews and D.C. Heins [ed.] Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, Okla.

Gatz, A.J. 1979*a*. Community organization in fishes as indicated by morphological features. Ecology, 60: 711–718.

Gatz, A.J. 1979*b*. Ecological morphology of freshwater stream fishes. Tulane Stud. Zool. Bot. 21: 91–124.

Gorman, O.T., and J.R. Karr. 1978. Habitat structure and stream fish communities. Ecology, 59: 507–515.

Hair, J.F., R.E. Anderson, R.L. Tatham, and B.J. Grablowsky. 1984. Multivariate data analysis. Macmillan Publishing Company, New York.

Humphries, J.M., F.L. Bookstein, B. Chernoff, G.R. Smith, R.L. Elder, and S.G. Poss. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291–308.

Ihssen, P.E., D.O. Evans, W.J. Christie, J.A. Reckahn, and R.L. DesJardine. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonis clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. 38: 1790–1807.

Karakousis, Y., C. Triantaphyllidis, and P.S. Economidis. 1991. Morphological variability among seven populations of brown trout *Salmo trutta* L. Evolution, 13: 807–817.

Keast, A., and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23: 1845–1874.

Kieffer, J.D., and P.W. Colgan. 1992. Differences in learning by foraging juvenile pumpkinseed and bluegill sunfish in a structured habitat. Environ. Biol. Fishes, 33: 359–366.

Layzer, J.B., and M.D. Clady. 1987. Phenotypic variation of young-of-year bluegills (*Lepomis macrochirus*) among microhabitats. Copeia, 1987: 702–707.

Matthews, W.J. 1985. Distribution of midwestern fishes on multivariate environmental gradients, with emphasis on *Notropis lutrensis*. Am. Midl. Nat. 113: 225–237.

Matthews, W.J. 1987. Geographic variation in *Cyprinella lutrensis* (Pisces: Cyprinidae) in the United States, with notes on *Cyprinella lepida*. Copeia, 1987: 616–637.

Misra, R.K., and I.-H. Ni. 1983. Distinguishing beaked redfishes (deepwater redfish, *Sebastes mentella* and Labrador redfish, *S. fasciatus*) by discriminant analysis (with covariance) and multivariate analysis of covariance. Can. J. Fish. Aquat. Sci. 40: 1507–1511.

Mittelbach, G.G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology, 65: 449–513.

Moyle, P.B., and D.M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Trans. Am. Fish. Soc. 114: 695–704.

Page, L.M., and D.L. Swofford. 1984. Morphological correlates of ecological specialization in darters. Environ. Biol. Fishes. 11: 139–159.

Pimentel, R.A. 1979. Morphometrics. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, 43: 223–225.

Riddell, B.E., and W.C. Leggett. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 38: 308–320.

Robison, H.W., and T.M. Buchanan. 1988. Fishes of Arkansas. The University of Arkansas Press, Fayetteville, Ark.

Roby, D., J.D. Lambert, and J.M. Sevigny. 1991. Morphometric and electrophoretic approaches to discrimination of capelin (*Mallotus villosus*) populations in the Estuary and Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 48: 2040–2050.

Schlosser, I.J., and L.A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and

fantail (*E. flabellare*) darters in a temporally variable environment. Oikos, 42: 229–238.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science (Washington, D.C.), 185: 27–37.

Shepherd, G. 1991. Meristic and morphometric variation in black sea bass north of Cape Hatteras, North Carolina. N. Am. J. Fish. Manage. 11: 139–148.

Strauss, R.E., and F.L. Bookstein. 1982. The truss: body form reconstruction in morphometrics. Syst. Zool. 31: 113–135.

Swain, D.P., B.E. Riddell, and C.B. Murray. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Can J. Fish. Aquat. Sci. 48: 1783–1791.

Taylor, E.B., and J.D. McPhail. 1985. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can J. Fish. Aquat. Sci. 42: 2020–2028.

Werner, E.E., and J.D. Hall. 1976. Niche shifts in sunfish: experimental evidence and significance. Science (Washington, D.C.), 191: 404–405.

Werner, E.E., J.D. Hall, D.R. Laughlin, D.J. Wagner, L.A. Wilsmann, and F.C. Funk. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34: 360–370.

Wiens, J.A., and J.T. Rotenberry. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecol. Monogr. 50: 287–308.

Wikramanayake, E.D. 1990. Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology, 71: 1756–1764.

Wimberger, P.H. 1992. Plasticity of fish body shape. The effects of diet, development, family and age in two species of *Geophagus* (Pisces: Cichlidae). Biol. J. Linn. Soc. 45: 197–218.

Winans, G.A. 1984. Multivariate morphometric variability in Pacific salmon: technical demonstration. Can J. Fish. Aquat. Sci. 41: 1150–1159.

Winn, H.E. 1958. Comparative reproductive behavior and ecology of fourteen species of darters (Pisces-Percidae). Ecol. Monogr. 28: 155–191.

Appendix

Names of species used in this study.

Common name	Code (used in Fig. 6)	Scientific name
Cyprinidae		
Largescale stoneroller	LSS	*Campostoma oligolepis*
Alabama shiner	ALS	*Cyprinella callistia*
Blacktail shiner	BTS	*Cyprinella venusta*
Striped shiner	STS	*Luxilus chrysocephalus*
Pretty shiner	PTS	*Lythrurus bellus*
Orangefin shiner	OFS	*Notropis ammophilus*
Silverstripe shiner	SLS	*Notropis stilbius*
Mimic shiner	MIS	*Notropis vollucellus*
Centrarchidae		
Redbreast sunfish	RED	*Lepomis auritus*
Bluegill	BLU	*Lepomis macrochirus*
Longear sunfish	LON	*Lepomis megalotis*
Percidae		
Greenbreast darter	GBD	*Etheostoma jordani*
Speckled darter	SPD	*Etheostoma stigmaeum*
Blackbanded darter	BBD	*Percina nigrofasciata*
Bronze darter	BZD	*Percina palmaris*

Allometry of home range size in lake and river fishes

Charles K. Minns

Abstract: A data set assembled from published literature supported the hypotheses that (*i*) home range size increases allometrically with body size in temperate freshwater fishes, and (*ii*) fish home ranges are larger in lakes than rivers. The allometric model fitted was home range = A·(body size)^B. Home ranges in lakes were 19–23 times larger than those in rivers. Additional analyses showed that membership in different taxonomic groupings of fish, the presence–absence of piscivory, the method of measuring home range, and the latitude position of the water bodies were not significant predictive factors. Home ranges of freshwater fish were smaller than those of terrestrial mammals, birds, and lizards. Home ranges were larger than area per fish values derived by inverting fish population and assemblage density–size relationships from lakes and rivers and territory–size relationships in stream salmonids. The weight exponent (B) of fish home range was lower than values reported for other vertebrates, 0.58 versus a range of 0.96–1.14. Lake–river home range differences were consistent with differences reported in allometric models of freshwater fish density and production.

Résumé : Un ensemble de données recueillies dans des documents publiés a permis de confirmer les hypothèses suivantes : (*i*) la taille du domaine vital augmente de façon allometrique en fonction de la taille du corps chez les poissons des eaux douces tempérées et (*ii*) les domaines vitaux des poissons sont plus grands dans les lacs que dans les cours d'eau. Le modèle allométrique ajusté était domaine vital = A·(taille du corps)^B. Dans les lacs, le domaine vital était 19–23 fois plus grand que dans les cours d'eau. Des analyses complémentaires ont montré que l'appartenance des poissons à différents groupements taxinomiques, la présence ou l'absence d'organismes piscivores, la méthode employée pour mesurer le domaine vital et enfin la latitude des masses d'eau ne constituaient pas des facteurs prédictifs significatifs. Chez les poissons d'eau douce, le domaine vital est plus petit que chez les mammifères terrestres, les oiseaux et les lézards. La superficie des domaines vitaux était supérieure à la superficie par poisson calculée en inversant les relations densité–taille chez les populations et assemblages de poissons des lacs et des cours d'eau et les relations territoire–taille chez les salmonidés lotiques. La composante poids (exposant B) du domaine vital des poissons était plus faible que celle mesurée pour d'autres vertébrés, avec 0,58 contre une fourchette de 0,96 à 1,14. Les différences de domaine vital entre les lacs et les cours d'eau correspondaient aux différences signalées dans les modèles allométriques de la densité et de la production des poissons dulcicoles.

[Traduit par la Rédaction]

Introduction

Beginning with McNab (1963), body size has been shown to be a significant determinant of home range size in mammals, birds, and reptiles (see Peters 1983 for a compilation of results). Allometric equations of home range (H) in relation to body weight (W) typically take the form $H = A \cdot W^B$ with two coefficients, a scalar A and an exponent B. McNab (1963) showed that home range size was an allometric function of body weight in mammals, with hunters having larger areas, a higher A value, than croppers. He also introduced the idea that home range size was linked to the metabolic requirements of mammals and therefore that the exponents (B) in allometric functions of body size should be similar. Schoener (1968) presented a similar analysis of feeding territories in birds. He found the exponents were higher in birds than those in mammals, the exponents were higher for predatory than herbivorous and omnivorous birds, and the areas for predatory birds were greater, i.e., the scalars were higher. Higher exponents indicate that home range increases more rapidly as body size increases. Turner et al. (1969) showed that home range was related to body size in lizards. Peters (1983) summarized the results for three groups, mammals, birds, and lizards, and, for the first two groups, showed that those eating animal food have larger home ranges than those eating plants. He also reported that exponents in allometric home range functions are generally higher than in allometric functions of metabolism.

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Table 1. Home range estimates for freshwater fish species in lakes and rivers.

Common name	Latin name	Length (mm)	Weight (g)	Home range	A[a]	B[b]	C[c]	D[d]	Lat. (°)	P[e]	O[f]	Reference
Largemouth bass	*Micropterus salmoides*	450	1500	9 520	L	T	C	B-	48.00	Y	N	Winter 1977
Largemouth bass		523	2489	14 000	L	T	C	B-	28.90	Y	N	Mesing and Wicker 1986
Largemouth bass		510	2330	10 100	L	T	C	B-	28.83	Y	N	Mesing and Wicker 1986
Largemouth bass		268	202	37 600	L	T	C	L2	42.42	Y	N	Savitz et al. 1983
Smallmouth bass	*Micropterus dolomieui*	392	853	2 000	L	T	C	L2	41.50	Y	Y	Savitz et al. 1993
Largemouth bass		268	202	9 200	L	T	C	L2	42.42	Y	N	Fish and Savitz 1983
Yellow perch	*Perca flavescens*	213	134	11 400	L	T	O	L3	42.42	N	N	Fish and Savitz 1983
Bluegill	*Lepomis macrochirus*	174	79	4 420	L	T	C	L2	42.42	N	N	Fish and Savitz 1983
Pumpkinseed	*Lepomis gibbosus*	153	82	4 950	L	T	C	L2	42.42	N	N	Fish and Savitz 1983
Largemouth bass		516	2125	126 000	L	T	C	B-	28.50	Y	N	Colle et al. 1989
White crappie	*Pomoxis annularis*	312	428	8 250	L	T	C	L2	40.33	N	N	Markham et al. 1991
Muskellunge	*Esox masquinongy*	830	3525	70 686	L	T	O	B-	44.50	Y	N	Crossman 1977
American eel	*Anguilla rostrata*	733	887	282 750	L	T	O	L3	44.50	Y	N	LaBar and Facey 1983
Brown trout	*Salmo trutta*	352	402	15 288.4	L	T	S	B-	56.10	N	N	Tytler et al. 1978
Bluegill		199	172	10 352.96	L	M	C	L2	42.25	N	N	Ball 1944
Yellow bullhead	*Ictalurus natalis*	239	202	6 145.74	L	M	O	L3	42.25	N	N	Ball 1944
Rock bass	*Ambloplites rupestris*	203	196	10 406.9	L	M	C	-2	45.50	N	N	Rodehoffer 1941
Yellow perch		177	78	6 947.92	L	M	O	-3	45.50	N	N	Rodehoffer 1941
Pumpkinseed		204	186	13 147.45	L	M	C	-2	45.50	N	N	Rodehoffer 1941
Smallmouth bass		292	370	7 316.54	L	M	C	-2	45.50	Y	N	Rodehoffer 1941
White crappie		296	423	158 000	L	T	C	B-	44.30	N	N	Guy et al. 1994
Cutthroat trout	*Oncorhynchus clarki*	222	99.2	101.25	R	M	S	W2	50.65	N	N	Miller 1957
Rainbow trout	*Oncorhynchus mykiss*	234	109	174	R	M	S	L2	45.67	N	N	Logan 1962
Brown trout		217	97	15.6	R	M	S	L2	40.50	N	Y	Bachman 1984
American eel		317	73	10 400	R	M	O	L3	31.35	Y	Y	Bozeman et al. 1985
Sculpin	*Cottus gobio*	76	5	18.75	R	M	O	L3	45.50	N	N	Downhower et al. 1990
Sculpin		76	5	77.5	R	M	O	L3	45.50	N	N	Downhower et al. 1990
Brown trout		125	52	45	R	M	S	L2	69.73	N	N	Hesthagen 1990
Atlantic salmon	*Salmo salar*	60	2	45	R	M	S	L2	69.73	N	N	Hesthagen 1990
Atlantic salmon		60	2	36	R	M	S	-2	45.18	N	N	Saunders and Gee 1964
Central stoneroller	*Campostoma anomalum*	150	34	116.11	R	M	O	-4	39.52	N	N	Mundahl and Ingersoll 1989
Muskellunge		830	3525	8 001	R	T	O	B-	44.50	Y	N	Crossman 1977
American eel		502	253	2 600	R	M	O	B-	31.35	Y	N	Helfman et al. 1983
Gila trout	*Salmo gilae*	163	47	343.7	R	M	S	L1	33.17	N	N	Rinne 1980,1982
Banded sculpin	*Cottus carolinae*	60	3	47	R	M	O	L3	35.50	N	N	Greenberg and Holtzman 1987
Mottled sculpin	*Cottus bairdi*	76	5	83.9	R	M	O	-3	35.17	N	N	Hill and Grossman 1987
Longnose dace	*Rhinichthys cataractae*	76	4	87.1	R	M	O	-4	35.17	N	N	Hill and Grossman 1987
Rosyside dace	*Clinostomus funduloides*	76	4	125.5	R	M	O	-4	35.17	N	N	Hill and Grossman 1987
Longear sunfish	*Lepomis megalotis*	95	16	97.5	R	M	C	L2	30.50	N	N	Gunning and Shoop 1963
Bluegill		97	16	174.2	R	M	C	L2	30.50	N	N	Gunning and Shoop 1963
American eel		362	108	126.5	R	M	O	L3	31.50	Y	N	Gunning and Shoop 1962
American eel		717	831	942	R	M	O	L3	31.50	Y	N	Gunning and Shoop 1962

Table 1 (*concluded*).

Common name	Latin name	Length (mm)	Weight (g)	Home range	A[a]	B[b]	C[c]	D[d]	Lat. (°)	P[e]	O[f]	Reference
Smallmouth bass		420	1134	1 963.5	R	T	C	L2	34.75	Y	N	Hubert 1981
Blacktail redhorse	*Moxostoma poecilurum*	366	562	282.1	R	M	O	L2	31.50	N	N	Gunning 1963
Brook trout	*Salvelinus fontinalis*	136	25	5 283.92	R	M	S	L2	44.67	N	Y	Shetter 1936
Brown trout		105.5	15.3	90	R	M	S	L3	52.25	N	N	Bridcut and Giller 1993

[a]Habitat: L, lake; R, river.
[b]Method: M, mark–recapture; T, telemetry.
[c]Taxonomic group: C, centrarchid; S, salmonid; O, other.
[d]Length–weight data. First character: -, none; B, both; L, length only; W, weight only. Second character: calculation method for missing data. See Materials and methods.
[e]Piscivore: yes or no.
[f]Outlier: yes or no. See Results for explanation.

Harestad and Bunnell (1979) presented a logical argument that habitats with higher productivity should result in smaller home ranges simply as a consequence of a smaller area being able to meet the metabolic needs of a consumer. They proposed that the exponent for a home range equation in mammals was greater than the metabolic one because habitat unit-area productivity declined with increasing size of consumer. They also showed that, in terrestrial ecosystems, home ranges were larger at higher latitudes where ecosystem productivity was lower.

Gerking (1953, 1959) brought the terms home range and territory to fish ecology from the avian and mammalian literature. He offered definitions for both: "Home range is the area over which an animal normally travels" and "Territory is any defended area." Grant and Kramer (1990) have shown relationships among territory size, body size, and density in stream salmonid populations. Equations showing the influence of body size, diet, and productivity on home range size have not been published for freshwater fishes, although there is considerable evidence that they have home ranges (Gerking 1953, 1959; Malinin 1972). Gerking (1953, 1959) reported evidence of home ranges in several groups of freshwater fishes including salmonids, catostomids, ictalurids, percids, and centrarchids. His experimental evidence was not suitable for the quantification of home ranges. Ryder and Pesendorfer (1989) highlighted many abiotic and biotic contrasts between lakes and rivers. Randall et al. (1995) showed how the production and abundance of freshwater fish are related to size and are higher in rivers than lakes. Thus, home range size in fishes might be expected to be smaller in rivers than in lakes.

Given the assessment of the factors that influence home range size in other biota and the likely role that habitat type or productivity might play, I compiled published measures of home range, and associated variables, for freshwater fishes in temperate aquatic ecosystems. These data were used to test two main hypotheses: (*i*) home range size increases with body size, and (*ii*) for similarly sized fish, home ranges in rivers are smaller than those in lakes. Auxiliary hypotheses were tested to assess the possible influence of taxonomic group, method of measuring home range size, presence–absence of piscivory, and latitude of the study site.

Materials and methods

The data analyzed in this study were obtained from an intense, but nonexhaustive literature review. I began with a key-word search of the *Aquatic Sciences and Fisheries Abstracts* on CD-Rom (Cambridge Scientific Abstracts, Bethesda, Md.), examined the papers identified there, and then examined older papers referred to in recent papers. I obtained 46 usable data sets, taking one datum per species per habitat.

Not all of the papers contained data in a form immediately useful for analyses; some calculation was required in many instances. In lotic studies, mark–recapture methods are mainly used and home range is usually calculated as the product of average longitudinal displacement and average stream width. In lentic studies, radio- and ultra-

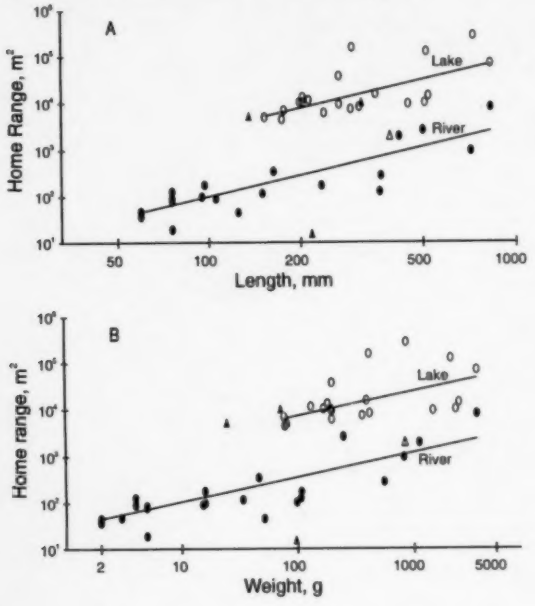


Fig. 1. Relationship of home range size (H, m^2) to (A) body length (L, mm) and (B) body weight (W, g) for freshwater fishes in lakes (open symbols) and rivers (solid symbols) using all raw data ($N = 46$). The lines are based on the following fitted regression models: $\log_e H = -2.41 + 3.30 \cdot HAB + 1.52 \cdot \log_e L$, and $\log_e H = 3.43 + 3.03 \cdot HAB + 0.53 \cdot \log_e W$ where HAB is 0 for rivers and 1 for lakes. Most data are marked with circles but possible outliers are indicated with triangles.

sonic telemetry methods are usual and the minimum convex polygon enclosing detection points defines the home range. In earlier lentic studies, mark–recapture methods were used and average displacement was taken as an estimate of the radius of a circle enclosing home range. Where multiple home range values were reported for a species in a particular place, I extracted a mean value. The number of fish used to obtain a value for each species in each habitat varied considerably and was related to the method of estimating home range. Mark–recapture methods typically involved many more individuals than telemetry methods.

Few of the studies provided both length and weight data for fish whose home ranges were estimated. If size frequency data were presented, a mean size was extracted or calculated. If a size range was given, the midpoint was used. If no size data were given, I used the midpoint of the adult length range reported for that species in Carlander (1969) or Scott and Crossman (1973), taking account of any relevant information given in the study reporting home range data.

If only one of length or weight was available after the initial data compilation, I used one of four methods to estimate the missing data. If Carlander (1969) contained site-specific data for the species involved, I used linear interpolation to estimate weights for lengths or vice versa (method 1). If site specific data were not found, I used the generalized tables in Carlander (1969) as in method 1 (method 2). In some instances where Carlander (1969) presented no data for a species, I used specific length–weight regression equations compiled at Glenora Fisheries Station (Donal A. Hurley, Ontario Ministry of Natural Resources, Picton, Ont., personal communication) (method 3). Finally, if no specific data were available, I used Carlander's (1969) universal length–weight equation ($W = L^3/10^5$, where W is measured in grams and L in millimetres) (method 4). There were 9 cases with no size information, 27 with only lengths, and 9 with both length and weight (Table 1).

Fish species in the accumulated raw data set were assigned to one of three taxonomic groups: salmonid, centrarchid, or other. Each species was designated as being piscivorous or not according to information in the source publications supplemented with material in Carlander (1969) and Scott and Crossman (1973). Gazetteers and atlases were used to estimate the latitude of each study where authors failed to provide coordinates.

The analysis of data was approached in two ways. First, the raw data were analyzed with one datum per species per habitat per study. Second, since the use of more than one datum for some species might unduly influence the analysis by a form of pseudoreplication, the data were log averaged by species and habitat type (lake or stream). The species data were analyzed with one datum per species per habitat.

Ordinary least squares (OLS) estimation methods were used to fit equations. Increasingly, structural regressions have been replacing predictive ones in the modelling of allometric relationships (Jensen 1986; McArdle 1988). The choice depends on an appreciation of the source and magnitude of uncertainty associated with dependent (Y) and independent (X) variables. McArdle (1988) recommends OLS when the relative error associated with X is expected to be less than one third that for Y. In this study, the level of error associated with home range size was expected to be much greater than that associated with body size. As allometric relationships usually exhibit increasing variation in the dependent variable with increasing size, home range and body size values were $\log_e$ transformed in all analyses.

For both the raw and species data sets, the analysis began with analyses of covariance to assess the influence of size and habitat on home range. Then a multiple regression model was fitted to provide the parameter values for the generic allometric model: $\log_e$ (home range) = $\log_e A + B \cdot \log_e$ (body size) + $C \cdot$(habitat). To examine the potential influence or confounding effects of other factors on the interpretation of the results, I expanded from the original analysis of covariance (ANCOVA) model involving habitat as a treatment and length as a covariate. I tested both the interaction with habitat and the direct effect of each additional factor. I used fish length rather than weight for these additional ANCOVA analyses because more of the data had lengths obtained from the source publications (Table 1). Covariance was analyzed and multiple linear regressions were calculated using SYSTAT version 5.0 for Windows (Wilkinson 1990).

Table 2. Results of analyses of covariance on home range size with habitat as an effect and body size as a covariate.

	Homogeneity of slopes		Size effect		Habitat effect		
	F_{SLOPES}	P	F_{SIZE}	P	F_{HAB}	P	R^2
			All data (N = 46)				
Length	0.02	0.89	31.21	<0.01	65.69	<0.01	0.80
Weight	0.17	0.69	21.36	<0.01	39.94	<0.01	0.77
			Species data (N = 29)				
Length	0.19	0.67	35.16	<0.01	51.61	<0.01	0.86
Weight	0.32	0.58	24.75	<0.01	34.77	<0.01	0.83

Results

Raw data

Forty-six home range values were obtained (Table 1), 21 in lakes and 25 in rivers, and these data constituted the raw data set. Each value represents one species in one habitat in one study. While the earliest datum came from Shetter (1936), most data were published in the 1980s. Total fish lengths ranged between 60 to 830 mm, while available live weights ranged between 2 and 3525 g. Home range size ranged between 2000 and 282 750 m^2 in lakes and between 16 and 10 400 m^2 in rivers and streams. The arithmetic mean home range size was higher in lake than river fish, 38 975 versus 1251 m^2. However, on average the lake fish were larger than river fish, 348 versus 225 mm length and 803 versus 281 g weight.

Centrarchids accounted for 15 of 21 lake values, while salmonids accounted for 9 of 25 river values (Table 1). In lakes, largemouth bass occurred 6 times and several other species occurred twice. In rivers, American eels occurred 4 times and brown trout 3 times. Piscivory was indicated for 10 lake values and 6 river values. Mark–recapture methods dominated in rivers and tracking with telemetry in lakes (Table 1).

The ranges of latitudes overlapped for the two groups of raw data, 28.50–56.10°N for lakes versus 30.50–69.73°N for rivers. Analysis of variance indicated that there was no significant difference between the mean latitudes (F = 0.22, P = 0.64).

Plots of home range size versus fish length and weight showed that body size was related to home range and that the home ranges in lakes were nearly always greater than those in rivers (Figs. 1A and 1B). Four values in the raw data set (marked by triangles in Figs. 1A and 1B) appeared to be outliers. Savitz et al. (1993) noted that their value for smallmouth bass was lower than others reported for bass. The authors attributed the difference to the smallness of the lake and the higher forage abundance. Bachman's (1984) value for brown trout appears to be closer to that expected for territory size (cf. Grant and Kramer 1990). Bozeman et al.'s (1985) value for eels comes from an estuarine ecosystem where productivity might be different from that in nonsaline lotic ecosystems but that does not explain the consistency of another value reported for eels in the same place by Helfman et al. (1983). Finally, Shetter's (1936) value for brook trout may be higher because migratory movements were included in the calculation; it was difficult to decide which data to use from the published material. None of these possible explanations for each outlier was conclusive and hence all data were retained in the raw and species-level analyses.

I began the statistical analysis of the raw data (N = 46) with analyses of covariance taking habitat as a treatment effect and body size as a covariate. With both length and weight, the F tests for homogeneity of slopes indicated that the slopes were not significantly different and the F tests for habitat and body size were significant (P < 0.001) (Table 2).

Next, I fitted a multiple regression model of $\log_e$ home range (H) with $\log_e$ length (L) and habitat as independent variables. That model explained 80% of the variation with both variables entering the model significantly (Table 3, model 1). The length exponent (B) in the allometric model was 1.52. When length was replaced by weight (W) in the model, the fit explained 77% of the variation (Table 2, model 2). The weight exponent was 0.55. Thus, the results of ANCOVA and regression analyses of the raw data set supported the primary hypotheses: home range size is related to body size in freshwater fishes and is consistently larger in lakes than in rivers.

Using ANCOVA, I examined the influence of four factors with the raw data set: taxonomic groups, piscivory, method of determining home range, and latitude. None of these factors was significant either in interaction with habitat or as a direct effect (Table 4).

Species data

By habitat, a single datum was obtained for each species, using the mean logarithms of length, weight, and home range values. The species data set contained 29 entries with 11 species in lakes and 18 in rivers. Most of the lake species were centrarchids, while centrarchids and salmonids together made up half the river species (Table 1). The averaging process reduced the spread of the data but did not alter the pattern observed in the raw data (Figs. 2A and 2B). Three of the four values that appeared to be outliers were

Table 3. Results of ordinary least-squares regression modelling of home range ($\log_e$ HR, m^2) in freshwater fishes with body size (total length ($\log_e$ LE, mm) or body weight ($\log_e$ WT, g)), and habitat (HAB: river = 0, lake = 1), using the raw and the species data sets.

			Regression statistics				
Model	Measurement	Parameter	Coeff.	SE	P	R^2	F_{regr}
		Raw data (N = 46)					
1	Length	$\text{Log}_e A$	−2.410	1.406	0.094	0.80	84.92
		C·HAB	3.296	0.407	0.000		
		B·$\log_e$ LE	1.523	0.273	0.000		
2	Weight	$\text{Log}_e A$	3.433	0.487	0.000	0.77	70.80
		C·HAB	3.026	0.479	0.000		
		B·$\log_e$ WT	0.527	0.114	0.000		
		Species data (N = 29)					
3	Length	$\text{Log}_e A$	−2.907	1.416	0.050	0.86	80.77
		C·HAB	3.137	0.437	0.000		
		B·$\log_e$ LE	1.651	0.278	0.000		
4	Weight	$\text{Log}_e A$	3.325	0.487	0.000	0.83	64.82
		C·HAB	2.978	0.505	0.000		
		B·$\log_e$ WT	0.578	0.116	0.000		

Note: The generic regression model is a logarithmic form of the allometric equation $\log_e$ (home range) = $\log_e A + B \cdot \log_e$ (body size) + C·(habitat).

Table 4. Results of additional analyses of covariance examining the influence of nonhabitat factors on home range size in freshwater fishes.

		Interaction with habitat		Direct effect	
	df[a]	F	P	F	P
	Raw data (N = 46)				
Taxonomic group	2,39	0.30	0.74	0.18	0.84
Piscivory	1,41	2.81	0.10	0.88	0.35
Method	1,41	1.19	0.28	1.26	0.27
Latitude	1,41	0.58	0.45	0.03	0.86
	Species data (N = 29)				
Taxonomic group	2,23	1.74	0.20	3.11	0.06
Piscivory	1,24	0.99	0.33	0.49	0.49

[a]Degrees of freedom.

involved in the averaging of raw values to obtain species values. Only one outlier remained in the averaged plots (Figs. 2A and 2B).

The analyses with the species data set produced similar results to those obtained with the raw data. In the ANCOVA, slopes were homogeneous for both length and weight, and size and habitat effects were significant in both cases (Table 2). The regression models accounted for higher percentages of variance, 86 and 83% with length and weight, respectively (Table 3). The coefficients obtained with raw and species data sets were similar, indicating that the presence of multiple values for certain species in the raw data set did not unduly influence the fitted models. The influence of taxonomic group and piscivory was assessed with the species data set by using ANCOVA and neither exhibited any significant effect (Table 4).

The allometric models fitted using the species data have exponents (B) for size of 1.65 and 0.58 for length and weight, respectively (Table 3). The habitat coefficients (C) for length and weight indicate that home ranges of freshwater fish are 19.6–23.0 times larger in lakes than in rivers. The allometric models obtained with the species data were used in the comparisons reported below.

Discussion

Before I offer any ecological interpretation of these results, Schoener's (1981) and others' concerns about errors in the estimation of home range should be considered. This is particularly important as mark–recapture methods dominate in studies of lotic ecosystems and telemetry in lentic ones. The analyses indicated that lake–river differences were not methodological. Schoener showed that the minimum convex polygon method used with telemetry data is sensitive to the number of sightings, and tends to overestimate home range when the number is small. Mark–recapture measures of displacement are often gathered using large-step distance intervals and then either the stream width is used to bound the area in rivers or the displacement is equated to the radius of a circle in lakes. In both methods, there is a tendency to overestimation and thus it is unlikely that methods can account for lake–river differences.

Fig. 2. Relationship of home range size (H, m^2) to (A) body length (L, mm) and (B) body weight (W, g) for freshwater fishes in lakes (open circles) and rivers (solid circles) using species data ($N = 29$). The lines are based on the fitted regression models: $\log_e H = -2.91 + 3.14 \cdot HAB + 1.65 \cdot \log_e L$, and $\log_e H = 3.33 + 2.98 \cdot HAB + 0.58 \cdot \log_e W$, where HAB is 0 for rivers and 1 for lakes.

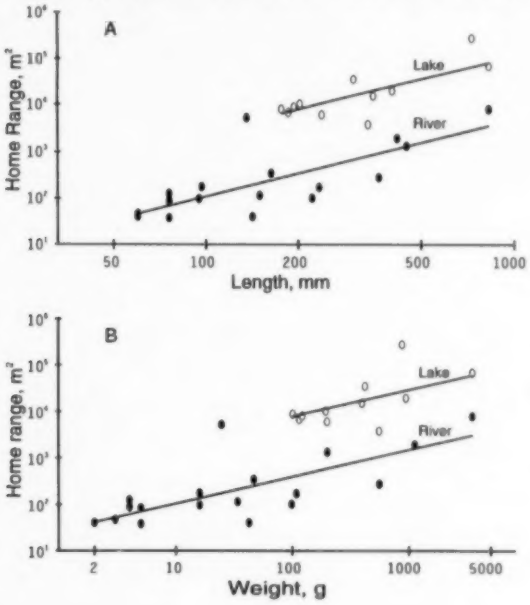
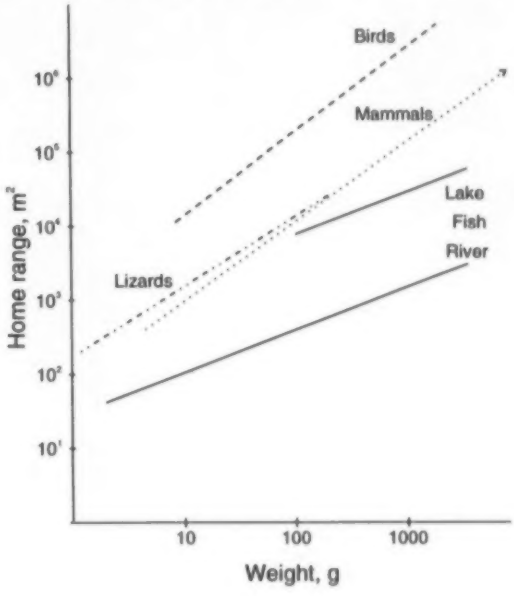


Fig. 3. Comparison of allometric models of home range for freshwater fishes in lakes and rivers with those reported for birds ($1000 \cdot W^{1.14}$, Schoener 1968), mammals ($80 \cdot W^{1.08}$, Harested and Bunnell 1979), and lizards ($171 \cdot 4W^{0.95}$, Turner et al. 1969).

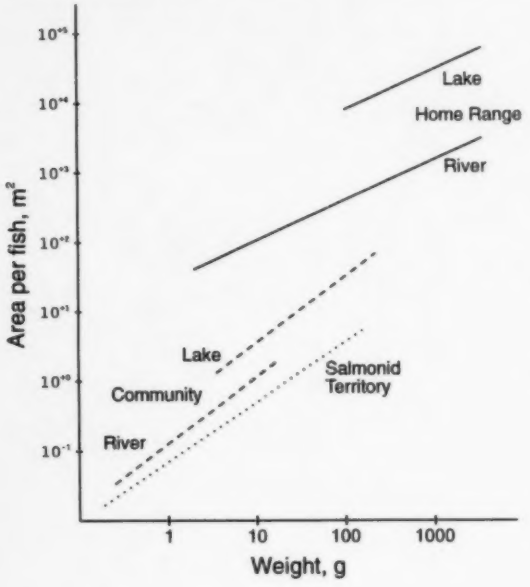


Over the weight range of fish in the compiled data, predicted home ranges of freshwater fishes lie below reported relationships for birds (Schoener 1968), mammals (Harested and Bunnell 1979), and lizards (Turner et al. 1969) (Fig. 3). The weight exponents for the nonfish biota range between 0.95 and 1.14 compared with 0.58 obtained here for freshwater fishes. The fish exponent was significantly different from 1 ($t = 3.64$, $P < 0.01$).

Following an approach used by Damuth (1981) and Peters (1983), I compared the home range model for freshwater fishes with the inverse of allometric density – body size models: the inverse of density per area equals area per animal. Randall et al. (1995) showed for freshwater fish communities that density declined with increasing mean fish weight, with rivers having greater densities than lakes when adjusted for mean weight. The inverted model with a weight exponent of 0.96 gives areas per fish below those for home range (Fig. 4). Area per fish was lower in rivers than in lakes. Bohlin et al. (1994) reported the allometric relationship between population density and body size in stream salmonids. The weight exponent for that inverted relationship was 0.98 and the line lies in the same location as the Randall et al. (1995) river line for fish communities. Calculations of area per fish based on population or community density assume that the population or community occupies the whole of the habitat area. If only a portion of the habitat is occupied as is indicated by the home range of individuals, the actual area per fish values will be lower than those estimated by inverting allometric density equations. Grant and Kramer (1990) developed a territory area – body size relationship for salmonids in streams, with a weight exponent of 0.86, which lies far below that for home range in rivers and below the line of area per fish in rivers (Fig. 4). The differences between the home range areas and areas per fish based on density or territory show the large spatial overlaps encountered by fishes in their home ranges. Thus, the home range model reported here for freshwater fishes is broadly consistent with previously developed allometric home range and density relationships.

McNab (1963) explored the role of metabolism in determining home range, proposing that the weight exponent in a logarithmic model should be similar to that for metabolism, 0.75. That and most subsequent studies have looked at animal groups that exhibit determinant growth where, at maturity, energy needs will be related to metabolism. With fishes, if the lake–river difference is ignored, the weight coefficient is 0.98 (Table 2, model 5), producing a situation comparable to that seen in other animal groups. However, the lake–river effect is present and is consistent with the observed differences in productivity (Randall et al. 1995). The weight power of 0.58 in fishes is significantly lower than the values for mammals, birds, and lizards, which range from 0.95 to 1.14 (Peters 1983). One possible reason for the inconsistency is that the growth patterns of fishes are different from those of the other vertebrate groups. Fish growth is indeterminant and the home range

Fig. 4. Comparison of allometric models of home range area for freshwater fishes in lakes and rivers with (*i*) area per fish in lakes and rivers estimated by inverting density – mean weight relationships among fish communities ($\log_e A = -2.07 + 1.13 \cdot HAB + 0.96 \cdot \log_e W$, where HAB is 0 for rivers and 1 for lakes, Randall et al. 1995), and (*ii*) territory size (T, m^2) as an allometric function of weight in stream salmonids ($\log_e T = -2.67 + 0.86 \cdot \log_e W$, Grant and Kramer 1990).



weight exponent might be expected to be closer to that for consumption of energy than to that for energy metabolism.

Fish growth is generally characterized as a balance of consumption and metabolism, with allowances for assimilation (Ursin 1967). The general growth equation for an individual fish is

$$dw/dt = H \cdot w^m - k \cdot w^n$$

$$\text{growth} = f\,(\text{consumption}) - g\,(\text{metabolism})$$

where w denotes weight. Ursin (1967) showed, in an extensive evaluation of the parameters of his growth model across many marine and freshwater fish species, that the consumption and metabolism weight exponents (m and n) were typically 0.56 and 0.83, respectively. The home range exponent is similar to that for consumption. Energy is consumed and provides for both metabolism and growth and that energy is gathered in the home range. The consistency of the home range and consumption weight exponents contradicts Harestad and Bunnell's (1979) inference for mammals that the home range weight exponent should be higher because average productivity declines as the home range grows. In freshwater fishes, the results suggest that average habitat productivity, as available food per unit area, does not decline as home range increases. Of course, this picture is made more complex, since as a fish grows larger, the size spectrum of potential food items shifts to larger sizes. The comparison here suggests the hypothesis that the weight exponent in an allometric model of home range is related to the consumption exponent in an allometric model of indeterminant growth.

In Grant and Kramer's (1990) model of territory area in stream salmonids, the weight exponent was 0.86, very close to Ursin's preferred value for the metabolic function. A territory is an actively defended area involving energy expenditure, and thus territory size might be expected to be functionally related to metabolic activity. At the population level, similar effects might explain why abundance – body size relationships, which have an inverted form of area per animal, have larger absolute exponents. Bohlin et al. (1994) showed in a detailed assessment of population density – body size relationships in stream salmonids that the weight exponent was 0.98 and indistinguishable from the weight exponent of metabolism, 0.92. Populations and communities at steady state are not accumulating biomass because on an aggregate basis mortalities offset recruitment and growth. Meanwhile, many of the constituent individuals will be growing, and assimilated consumption allows metabolism and growth. Hence overall, population or community abundance is more likely to be related to metabolism as, at steady state, biomass is at a maximum, and assimilated consumption only matches metabolic needs and mortality and emigration losses.

The lake–river differences in the home range area of freshwater fishes are consistent with differences in abundance and production of fish assemblages (Randall et al. 1995). Among the compiled data, there are instances for brown trout (*Salmo trutta*), American eels (*Anguilla rostrata*), and centrarchids where home ranges have been measured in both lakes and rivers, producing results that are qualitatively consistent with the fitted allometric models (Tables 3 and 1). In Crossman (1977), a single muskellunge (*Esox musquinongy*) occupied different-sized home ranges in a lake versus a river. The ratio of lake:river home ranges by length is 23:1 and by weight 19.6:1. Rivers have higher unit-area productivity rates than lakes and hence home ranges would be expected to be smaller if home range is proportional to food supply (Harested and Bunnell 1979; Ryder and Pesendorfer 1989). Randall et al. (1995) found that freshwater fish community density and production varied inversely with mean body weight and that lake:river ratios were 0.33 and 0.67, respectively. Home range sizes are larger in the habitat supporting lower fish densities and lower production. The size differences of the ratios can be explained by differences in the way fishes acquire food. In streams and rivers, drift often makes an important contribution to food intake, effectively expanding upstream the area whose productivity is exploited by fishes. Allochthonous production is a primary source of food energy in rivers, while autochthonous production is the primary source in lakes (Ryder and Pesendorfer 1989). In lakes, fishes must visit food-producing areas to obtain their food, while in rivers food may be brought to them by the current. This explanation may also explain why fish production:biomass ratios are greater in rivers than lakes (Randall et al. 1995). Lake fishes have to move further to obtain the food they consume and hence have to expend a greater proportion of the energy acquired on

metabolism, leaving less for growth. Thus, the instantaneous growth rates of fishes in rivers should be greater than those of fishes in lakes.

The predictive allometric model of home range in freshwater fishes can be used to guide the conservation and management of fish habitat. The home range is the area from which an individual fish obtains its food energy and this area should help define the frame for habitat assessment when proposed human developments impinge on freshwater ecosystems. Assessments usually focus on the point locations of fishes and developments. Assessments should consider the habitat areas used by each fish for such activities as spawning, feeding, and migrating, and the area modified, directly and indirectly, by a development. Assessment studies are rarely of sufficient duration and intensity that the full spatial extent of habitat usage is mapped onto the area modified by the project. The predictive home range regression models developed here for lakes and rivers can be used to define the area in which a particular site development needs to be assessed, though some adjustment may be necessary in rivers to allow for the role of drift. As an example, given the overlap among individual home ranges, the area of a proposed habitat modification could be surrounded by an overlapping series of borders with widths equal to the radii of circles with areas equal to the home ranges of fishes living in the vicinity of the proposed habitat modification. The fish sizes used with the equation would be determined by the species and size ranges occupying that habitat. This approach would explicitly recognize that the impact of any development extends beyond its immediate confines. This individual fish approach might be coupled with an examination of the area needed to support self-sustaining populations of the species occurring within the project's zone of influence.

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References

Bachman, R.A. 1984. Foraging behaviour of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. 113: 1–32.

Ball, R.C. 1944. A tagging experiment on the fish population of Third Sister Lake, Michigan. Trans. Am. Fish. Soc. 74: 360–369.

Bohlin, T. C., Dellefors, U. Faremo, and A. Johlander, 1994. The energetic equivalence hypothesis and the relation between population density and body size in stream-living salmonids. Am. Nat. 143: 478–493.

Bozeman, E.L., G.S. Helfman, and T. Richardson. 1985. Population size and home range of American eels in a Georgia tidal creek. Trans. Am. Fish. Soc. 114: 821–825.

Bridcut, E.E., and P.S. Giller. 1993. Movement and site fidelity in young brown trout, *Salmo trutta*, populations in a southern Irish stream. J. Fish Biol. 43: 889–899.

Carlander, K.D. 1969. Handbook of freshwater fishery biology. Vols. I and II. 3rd ed. Iowa State University Press, Ames, Iowa. 752 + 431 p.

Colle, D.E., R.L. Cailteux, and J.V. Shireman. 1989. Distribution of Florida largemouth bass in a lake after elimination of all submerged aquatic vegetation. N. Am. J. Fish. Manage. 9: 213–218.

Crossman, E.J. 1977. Displacement, and home range movements of muskellunge determined by ultrasonic tracking. Environ. Biol. Fishes 1: 145–158.

Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. Biol. J. Linn. Soc. 15: 185–193.

Downhower, J.F., P. Lejeune, P. Gaudin, and L. Brown. 1990. Movements of the chabot (*Cottus gobio*) in a small stream. Pol. Arch. Hydrobiol. 37: 119–126.

Fish, P.A., and J. Savitz. 1983. Variations on home ranges of largemouth bass, yellow perch, bluegills, and pumpkinseeds in an Illinois lake. Trans. Am. Fish. Soc. 112: 147–153.

Gerking, S.D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, 34: 347–365.

Gerking, S.D. 1959. The restricted movement of fish populations. Biol. Rev. Cambridge Philos. Soc. 34: 221–241.

Grant, J.W.A., and D.L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. 47: 1724–1737.

Greenberg, L.A., and D.A. Holtzman. 1987. Microhabitat utilization, feeding periodicity, home range and population size of the banded sculpin, *Cottus carolinae*. Copeia, 1987: 19–25.

Gunning, G.E. 1963. The concepts of home range and homing in stream fishes. Ergeb. Biol. 26: 202–215.

Gunning, G.E., and C.R. Shoop. 1962. Restricted movements of the American eel, *Anguilla rostrata* (LeSueur), in freshwater streams, with comments on growth rate. Tulane Stud. Zool. 9: 265–272.

Gunning, G.E., and C.R. Shoop 1963. Occupancy of home range by longear sunfish, *Lepomis m. megalotis* (Rafinesque), and bluegill, *Lepomis m. macrochirus* Rafinesque. Anim. Behav. 11: 325–330.

Guy, C.S., D.W. Willis, and J.J. Jackson. 1994. Biotelemetry of white crappies in a South Dakota glacial lake. Trans. Am. Fish. Soc. 123: 63–70.

Harestad, A.S., and F.L. Bunnell. 1979. Home range and body weight: a reevaluation. Ecology, 60: 389–402.

Helfman, G.S., D.L. Stoneburner, E.L. Bozeman, P.A. Christian, and R. Whalen. 1983. Ultrasonic telemetry of American eel movements in a tidal creek. Trans. Am. Fish. Soc. 112: 105–110.

Hesthagen, T. 1990. Home range of juvenile Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in a Norwegian stream. Freshwater Biol. 24: 63–67.

Hill, J., and G.D. Grossman. 1987. Home range for three North American stream fishes. Copeia, 1987: 376–380.

Hubert, W. 1981. Spring movements of smallmouth bass in the Wilson Dame tailwater, Alabama. J. Tenn. Acad. Sci. 56: 105–106.

Jensen, A.L. 1986. Functional regression and correlation analysis. Can. J. Fish. Aquat. Sci. 43: 1742–1745.

LaBar, G.W., and D.E. Facey. 1983. Local movements and inshore population sizes of American eels in Lake Champlain, Vermont. Trans. Am. Fish. Soc. 112: 111–116.

Logan, S.M. 1962. Winter observations on bottom organisms and trout in Bridger Creek, Montana. Trans. Am. Fish. Soc. 92: 140–145.

Malinin, L.K. 1972. Home range and homing instinct of fish. (Zool. Zh. 48: 381–391, 1969). Fish. Res. Board Can. Transl. Ser. 2050: 22 p.

Markham, J.L., D.L. Johnson, and R.W. Petering. 1991. White crappie summer movements and habitat use in Delaware Reservoir, Ohio. N. Am. J. Fish. Manage. 111: 504–512.

McArdle, B.H. 1988. The structural relationship: regression in biology. Can. J. Zool. 66: 2329–2339.

McNab, B.K. 1963. Bioenergetics and the determination of home range size. Am. Nat. 97: 133–140.

Mesing, C.L., and A.M. Wicker, 1986. Home range, spawning migrations, and homing of radio-tagged Florida largemouth bass in two central Florida lakes. Trans. Am. Fish. Soc. 115: 286–295.

Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. J. Fish. Res. Board Can. 14: 687–691.

Mundahl, N.D., and C.G. Ingersoll. 1989. Home range, movements, and density of the central stoneroller, *Campostoma anomalum*, in a small Ohio stream. Environ. Biol. Fishes, 24: 307–311.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge. 329 p.

Randall, R.G., J.R.M. Kelso, and C.K. Minns. 1995. Fish production in freshwaters: are rivers more productive than lakes? Can. J. Fish. Aquat. Sci. 52: 631–643.

Rinne, J.N. 1980. Spawning habitat and behaviour of Gila trout, a rare salmonid of the southwestern United States. Trans. Am. Fish. Soc. 109: 83–91.

Rinne, J.N. 1982. Movement, home range, and growth of a rare southwestern trout in improved and unimproved habitats. N. Am. J. Fish. Manage. 2: 150–157.

Rodehoffer, I.A. 1941. The movements of marked fish in Douglas Lake, Michigan. Pap. Mich. Acad. of Sci. Arts Lett. 26: 265–280.

Ryder, R.A., and J. Pesendorfer. 1989. Large rivers are more than flowing lakes: a comparative review. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. No. 106. pp. 65–85.

Saunders, R.L., and J.H. Gee. 1964. Movements of young Atlantic salmon in a small stream. J. Fish. Res. Board Can. 21: 27–36.

Savitz, J., P.A. Fish, and R. Weszely. 1983. Effects of forage on home-range size of largemouth bass. Trans. Am. Fish. Soc. 112: 772–776.

Savitz, J., L.G. Bardygula, T. Harder, and K. Stuecheli. 1993. Diel and seasonal utilization of home ranges in a small lake by smallmouth bass (*Micropterus dolomieui*). Ecol. Freshwater Fishes, 2: 31–39.

Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology, 49: 123–141.

Schoener, T.W. 1981. An empirically based estimate of home range. Theor. Popul. Biol. 20: 281–325.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. No. 184. 966 p.

Shetter, D.S. 1936. Migration, growth rate, and population density of brook trout in the North branch of the Au Sable River, Michigan. Trans. Am. Fish. Soc. 66: 203–210.

Turner, F.B., R.I. Jennrich, and J.D. Weintraub. 1969. Home range and body size of lizards. Ecology, 50: 1076–1081.

Tytler, P., D. Machin, F.G.T. Holliday, and I.G. Priede. 1978. A comparison of the patterns of movement between indigenous and displaced brown trout (*Salmo trutta* L.) in a small shallow loch. Proc. R. Soc. Edinb. Sect. B Biol. Sci. 76: 245–268.

Ursin, E. 1967. A mathematical model of some aspects of fish growth, respiration, and mortality. J. Fish. Res. Board Can. 24: 2355–2453.

Wilkinson, L. 1990. SYSTAT: the system for statistics. Systat, Inc., Evanston, Ill. 667 p.

Winter, J.D. 1977. Summer home range movements and habitat use by four largemouth bass in Mary Lake, Minnesota. Trans. Am. Fish. Soc. 106: 323–330.

Response of *Mysis relicta* population dynamics and productivity to spatial and seasonal gradients in Lake Ontario

Ora E. Johannsson

Abstract: Spatial and temporal patterns of production, density, reproductive status, and size composition of *Mysis relicta* in Lake Ontario were analyzed in relation to predation and physical conditions. Two whole-lake (May, November) surveys and one partial (August) survey were conducted in 1990. Spatial patterns were related to lake depth. Abundance increased with depth of sampling stations, particularly between 20 and 100 m. At station depths >100 m, the percentage of females carrying eggs and mean female size were constant, but the number of eggs per female increased with station depth. During the winter, the density–depth relationship weakened, apparently through the action of storms and currents, but strengthened again during the summer. Mysids >9 mm in length tended to move to deeper water during the summer. The distributions of predatory fish (alewife, smelt, and sculpin) suggest that depth-related patterns in the mysid population may be due to differences in predation rates with depth and season as well as to horizontal movement. Whole-lake production was estimated to be between 412.91 and 506.82 $\times 10^8$ g dry weight: most production occurred between 100 and 200 m depth. Growth rate was similar in all regions of the lake.

Résumé : Les profils spatiaux et temporels de la production, de la densité, de l'état reproductif et de la composition par taille des *Mysis relicta* du lac Ontario ont été analysés en relation avec la prédation et les conditions physiques. Deux relevés concernant l'ensemble du lac (mai, novembre) et un relevé partiel (août) ont été effectués en 1990. Les profils spatiaux étaient en rapport avec la profondeur du lac. L'abondance augmentait avec la profondeur des stations d'échantillonnage, particulièrement entre 20 et 100 m. Aux stations de profondeur supérieure à 100 m, le pourcentage de femelles oeuvées et la taille moyenne des femelles étaient constants, mais le nombre d'oeufs par femelle augmentait avec la profondeur de la station. Pendant l'hiver, la relation densité–profondeur s'atténuait, ce qui semble être dû à l'action des tempêtes et des courants, mais elle se renforçait de nouveau en été. Les mysidés de plus de 9 mm de longueur se déplaçaient vers les eaux profondes pendant l'été. Les distributions des poissons prédateurs (gaspareau, éperlan, chaboisseau) font apparaître que les profils liés à la profondeur dans la population de mysidés peuvent être dus à des différences de taux de prédation selon la profondeur et la saison ainsi qu'au déplacement horizontal. On a estimé que la production de l'ensemble du lac se situait entre 412,91 et 506,82 $\times 10^8$ g en poids sec : la plus grande partie de cette production se retrouvait entre 100 et 200 m de profondeur. Le taux de croissance était similaire dans toutes les régions du lac.

[Traduit par la Rédaction]

Introduction

The flux of energy through ecosystems is governed not only by nutrient inputs and the seasonal patterns of temperature and hydrology, but also by the biological structure of the ecosystem, the relative timing of biological events, and the spatial structure of the environment. In large lakes, trophic relationships change through the year in connection with seasonal changes in spatial overlap among species and with gradients in physical and chemical variables, such as oxygen levels, temperature, and nutrient concentrations. These seasonally changing spatial patterns need to be incorporated into our descriptions of energy flow if we hope to determine the major pathways, the weak links, and how the system will be affected by change.

The opossum shrimp, *Mysis relicta*, is a benthic–pelagic invertebrate that inhabits off-shore, hypolimnetic waters. Mysids avoid light, remaining in deep water during the day, often just above or in the bottom substrate (Bowers et al. 1990), although in extremely low light levels, they can remain totally pelagic (Morgan et al. 1978). During the day, they eat algae, detritus, and the occasional invertebrate (McWilliam 1970 in Grossnickle 1982; Lasenby and

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Langford 1973; Parker 1980; Lasenby and Furst 1981). At night, mysids migrate up through the water column where, depending on the lake and time of year, they feed on zooplankton or algae, often diatoms (Grossnickle 1982). Mysids, in turn, are preyed upon by fish, particularly cold-water benthivores (Lasenby et al. 1986; Naesje et al. 1987; McDonald et al. 1990; Kjellberg et al. 1991).

Mysid production has been measured in three of the Laurentian Great Lakes: Michigan (Sell 1982), Huron (Sell 1982), and Ontario (Shea and Makarewicz 1989; Johannsson 1992). In these studies production was estimated either at a single site or at sites greater than a certain depth. This approach provides no information on spatial patterns of mysid production, which is required for trophic models of whole-lake ecosystems.

Mysid abundance increases with depth (Reynolds and DeGraeve 1972; Carpenter et al. 1974; Morgan and Beeton 1978; Johannsson 1992), and mysids can actively migrate (Reynolds and DeGraeve 1972; Morgan and Threlkeld 1982; Moen and Langeland 1989) or be moved passively by currents (Grossnickle and Morgan 1979; Salemaa et al. 1986; Shea and Makarewicz 1989; Bowers et al. 1990; Kjellberg et al. 1991; Johannsson 1992). Johannsson (1992) suggested that mysid size-frequency distributions might also change with depth. Therefore, relationships between depth and production need to be investigated.

Predation on mysids is patchy in time and space. Fish that consume mysids do not always co-occur with the mysid population throughout the year (e.g., alewife (*Alosa pseudoharengus*), Olson et al. 1988; Schaner et al. 1989; Mills et al. 1992) or they may overlap with only a portion of the population (e.g., slimy sculpin (*Cottus cognatus*), Brandt 1986). The size of mysid eaten and the proportion of production available to predators depends on the spatial and temporal distributions and size structures of both mysid and predator populations. Conversely, predators impose a spatial pattern of mortality on the mysid population that affects mysid distribution and production.

In this paper, I assess spatial and temporal patterns in *Mysis relicta* population dynamics and production in Lake Ontario and their implications for energy transfer in the system.

Materials and methods

Sample collection and processing

Three cruises were undertaken in 1990: May 22–31, July 30 – August 3, and October 29 – November 9. A total of 55 stations were sampled per cruise: 10 stations per 50 m depth range with five additional stations in depths less than 10 m (Fig. 1). One sample was collected per station. This work with mysids was part of a larger study of energy transfer in Lake Ontario (the Lake Ontario Trophic Transfer Study (LOTT)) and 32 of the stations were common to all LOTT studies. These sampling stations were located along six north–south transects spaced evenly down the lake. Other stations were added to distribute sampling effort in each depth range evenly about the axes of the lake (Fig. 1). Station depths were not always as expected from hydrographic maps; the number of replicates per depth range varied from 7 to 12.

The summer cruise (July 30 – August 3) was restricted in time: I collected samples only along the midlake transect, which had a maximum depth of 170 m, and from the deep trench (>200 m in depth). Two stations were added to the midlake transect to give two stations per depth range. During this cruise, four replicates were collected at each station to increase the precision of the abundance estimates, given the reduction in station number, and to obtain some estimate of variability.

We employed the sampling protocol recommended by Nero and Davies (1982). A 1-m^2, square net, constructed of 1-mm nitex mesh with a 250-μm cod end (Nero 1982), was lowered to within 1–1.5 m of the bottom, allowed to rest for 30 s to permit the redistribution of mysids in the overlying water, and then raised to the surface at 1/3 to 1/2 $m \cdot s^{-1}$. All samples were taken between dusk plus 1 h and dawn minus 1 h. The ship's deck lights were off while the sample was collected. The animals were preserved in 8% Formalin. Filtering efficiency of the net was not measured; a similar net deployed in the same manner by Nero and Sprules (1986) had an efficiency of 87%. Therefore, abundance and production estimates may be underestimated by approximately 13%.

All samples were enumerated completely, and body length, sex, and number of eggs were recorded for 100 randomly selected individuals from each sample. Body length was measured from the tip of the rostrum to the apical cleft of the telson. Because the body of preserved animals assumes a V shape, the body length was measured in two sections and the values were summed. The image of the organism was projected onto a digitization pad, and its length determined from the coordinates. The system was calibrated at the beginning of each sample. Sex was determined from the structure of the fourth pleopod, which thickens and bifurcates in males (Balcer et al. 1984).

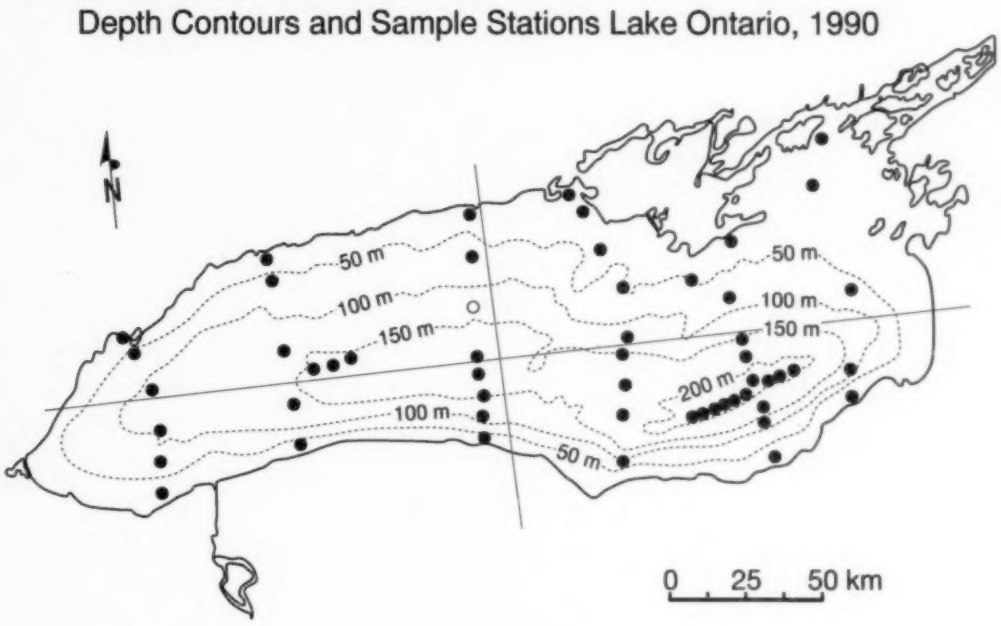
Abundance and life history

The abundance data were first examined graphically using a Geographic Information System (GIS) to depict spatial variation in abundance in the lake. Each station was assigned an area of the lake on the basis of the nearest-neighbour technique. Mysid density at each station was assumed to represent average densities in the surrounding polygon.

To examine the effect of location within the lake on abundance, the distances of the stations from the north–south and east–west axes of the lake (Fig. 1) were calculated. The ability of location and station depth to predict mysid abundance was examined by multiple regression analysis after the independent variables (distance, station depth) were standardized, using z scores, and the dependent variable (abundance) was transformed ($\log(x + 1)$).

The relationship between mysid density and station depth changed between the 75 and 125 m depth contours but insufficient data existed to define a precise breaking point. The data were transformed ($\log(x + 1)$) and regression analyses of abundance with station depth were performed on two subgroups of stations: those between 20 and 100 m, and those >100 m.

Fig. 1. Map of Lake Ontario indicating depth contours, north–south and east–west axes of the lake, and the location of mysid sampling stations. ○, reference station 41 from the Long Term Biological Monitoring Program (Department of Fisheries and Oceans).



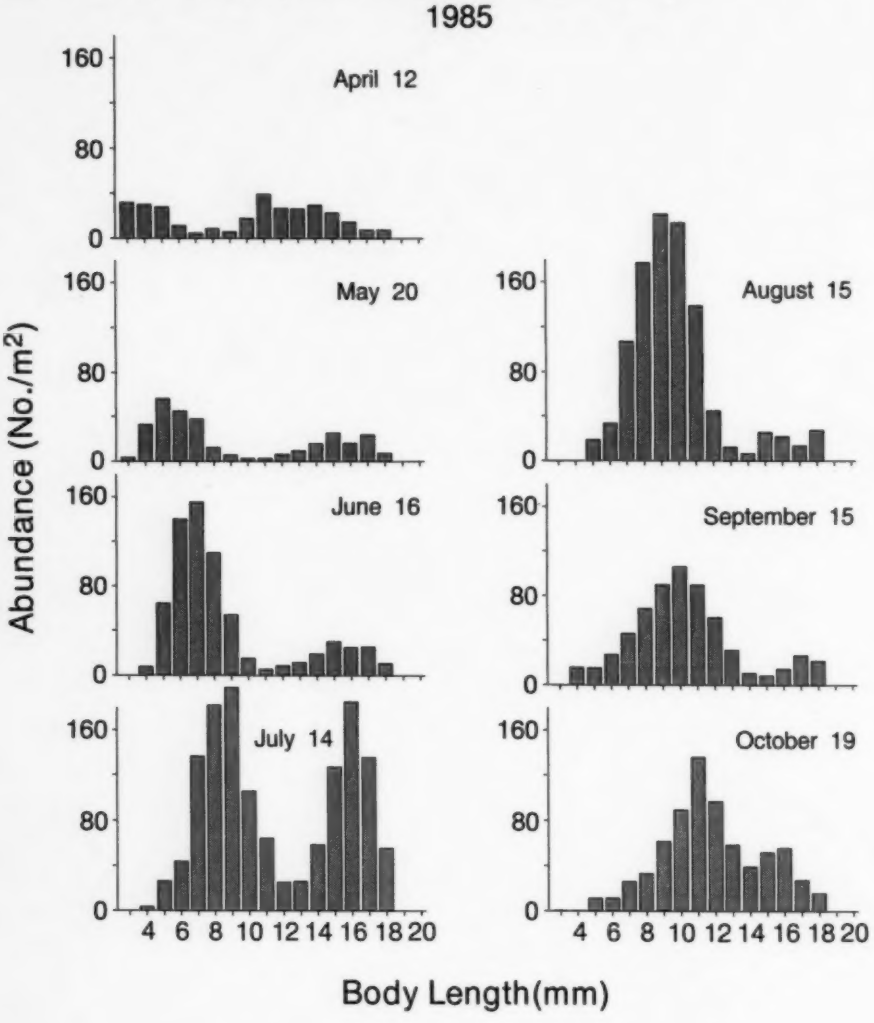
The size structure of mysid populations can be complex and variable. A 4-year study of mysids in Lake Ontario at the Department of Fisheries and Oceans' Long Term Biomonitoring (Bioindex) station (station 41 at 125 m depth on the midlake transect; Fig. 1) showed that the mysid population in this region has a 24-month generation time from conception to first reproduction, that the majority of the population reproduces in the late autumn, and that reproduction spans several months (Fig. 2, from Johannsson 1992). This bimodal pattern of cohort development was not as clear in Lake Ontario in the 1972 whole-lake size-frequency distributions of Carpenter et al. (1974, in Johannsson 1992), and more complex population structures have been described elsewhere (Morgan and Beeton 1978). Therefore, the size structure of the population was compared across depth ranges. Size-frequency distributions (m^{-2}) were summed for all stations within each 50-m contour except 0–50 m where few mysids were found. For each cruise, the size-frequency distributions from the four depth ranges were compared using a G test (Sokal and Rohlf 1969). Because significant differences were observed (G = 90 to 533, p <0.05 to <0.001), the densities of mysids in three size categories, which roughly equate to spring young-of-the-year, yearlings, and mature females during the period April to October (<9 mm, 9–15 mm, >15 mm in length; Johannsson 1992), were compared across depth contours by one-way analysis of variance.

Migration can also alter depth-related relationships. Expected size distributions were calculated for August and November from the May and August data, respectively, using growth rates determined previously for Lake Ontario (Johannsson 1992). Expected mysid abundances in each sample were summed across 3-mm size-classes. Within each depth range, the number of mysids expected was compared with the number observed by using a t test or a non-parametric version of the t test, based on the median and sample interquartile range (Mosteller and Tukey 1977), if the data were not normally distributed. Changes in abundance within a size-class were then compared across depth ranges.

Reproductive status and growth rate were compared throughout the lake. I compared across depth ranges (*i*) the proportion of mature females (≥14 mm) carrying eggs or embryos in May and November, (*ii*) the mean number of eggs per female, (*iii*) the mean size of females, and (*iv*) the proportion of females ≥17 mm in length. One-way analysis of variance was applied in comparisons *i*, *iii*, and *iv*; analysis of covariance (ANCOVA) was used in comparison *ii* because the number of eggs carried by a female is partly dependent on her size (e.g., Morgan 1980; Adare 1992; Beeton and Gannon 1991). All females carrying embryos were removed from comparison *ii* because Morgan (1980) showed that embryos can be lost from the marsupium during development. Too few data (n = 3) from 50–100 m stations were available for these analysis.

The clear bimodal pattern of cohort development in Lake Ontario at station 41 allowed Johannsson (1992) to calculate growth rates of the spring generation. To compare growth across depth ranges and with this earlier study, peak abundances in the size-frequency data from May and November were compared with the expected peaks from derived size-frequency distributions based on Johannsson's growth rates.

Fig. 2. Seasonal size-frequency distributions of mysids from a 125 m depth site in Lake Ontario: station 41, 1985. The large increases in abundance in July of mysids of all sizes and decrease in August of larger mysids are immigration and emigration events.



Production

Production was estimated using Menzies' (1980) modification of the size-frequency method of Hynes. The presence of overlapping cohorts and the long reproductive period preclude the use of cohort analysis to calculate production. The long time between sampling periods, particularly over the winter, reduces the accuracy of production estimated for the average population in each interval. The size-frequency method, as applied in the present study, estimates production within ±15% of true production assuming mortality rates of ≤0.5%/day (Iversen and Dall 1989); that is, with the equivalent of six sampling periods during the cohort production interval, with over 10 size-classes, and with a known growth pattern. In the size-frequency method, biomass lost between size-classes is summed over the year (November to November) to calculate production. In 1990 the mysid population was assumed to be in equilibrium and the November data for 1990 were also used to represent the November 1989 conditions.

$$\text{Production} = \Sigma_{j=1}^{i} (N_j - N_{j+1}) \times (W_j W_{j+1})^{1/2}$$

and

$$N_j = in_j \times P_{ej}/P_{aj} \times 365/\text{CPI}$$

where i is the number of size categories, N_j is the number of mysids that developed into size category j in a year, W_j is the mean weight of mysids in the jth category, n_j is the mean number of mysids in category j, P_{ej} is the estimated

proportion of the life cycle spent in the *j*th category ($1/i$), P_{aj} is the actual proportion of the life cycle spent in the *j*th category, and CPI is the cohort production interval in days from hatching to reaching the largest size-class.

Without winter samples I could not follow reproduction closely enough to determine the number of eggs produced or the number hatched. Therefore, I assumed that all females >14 mm in length in November successfully carried and released 10 young. This figure was set at less than half the average number of eggs carried per female to compensate for loss of eggs from the marsupium and mortality of egg-bearing females. A newly released embryo is 3–4 mm in length. Mysids were sampled quantitatively once they reached 7 mm in length; therefore, production was calculated from 3 to 7 mm directly.

As Johannsson (1992) pointed out, the number of individuals in size-classes (i.e., N_j) normally grown through during the winter months, is underestimated by this method of calculation when winter samples are not collected (Table 1). This results in positive and then negative production estimates between size-classes as the estimated abundances first drop and then rise again over the 9- to 14-mm size ranges. Therefore, I calculated production directly between the 9- and 14-mm size classes.

Monthly samples for mysids were collected from April until October at station 41 by staff of the Bioindex program (Fig. 1). Four replicates were collected each month. The sampling and processing methodologies were identical to those used in the present study. Production was calculated for station 41 in 1990 and compared with the whole-lake estimate of production for this depth range.

Table 1. The number of mysids in four depth ranges passing through each 1-mm size-class during the year; that is, the N_j estimates from the production calculations.

Size-class (mm)	Density of mysids (No./m^2)			
	50–100 m	100–150 m	150–200 m	>200 m
Newborn	191	1144	2336	2242
7.0–7.9	81	294	246	385
8.0–8.9	78	288	276	360
9.0–9.9	81	289	324	357
10.0–10.9	74	108	118	165
11.0–11.9	66	93	137	138
12.0–12.9	53	101	123	145
13.0–13.9	58	220	311	324
14.0–14.9	61	222	402	404
15.0–15.9	75	256	451	439
16.0–16.9	45	233	383	373
17.0–17.9	37	177	213	314
18.0–18.9	16	142	153	242
≥19.0	12	126	170	230

Note: The number of newborn was estimated from the number of females. Mysids <7.0 mm in length were not sampled efficiently and therefore were not included. Lack of winter sampling underestimated the 9.9–13.9 mm mysids and they have been separated in the table. See text for more detailed discussion of assumptions and limitations.

Results

Abundance and size-frequency distributions

Mysid density increased with station depth, but the spatial pattern varied seasonally. There was greater spatial heterogeneity of abundance in the spring than in the autumn, with higher spring densities stretching from the deep trough (≥200 m) toward the northwest (Fig. 3). The coefficient of variation of mean abundance from station depths >100 m was 48% in November compared with 70% in May. In November, high densities were more closely related to station depth.

At no time did geographic location account for any significant variability in the data. If the analysis were restricted either to depths >100 m or to depths <100 m, the results were the same. Depth was the only important factor. Consequently, no further analyses were pursued with the geographic variables.

Abundance increased with station depth between 20 and 100 m in all seasons (Fig. 4). Although r^2 increased from spring to fall, indicating that the relationship between station depth and abundance strengthened as the season progressed, no significant differences in the slopes or adjusted means of the abundance – station depth relationships were found using ANCOVA. Beyond 100 m depth, abundance was not related to station depth in spring and summer but did increase with station depth in the autumn (Fig. 4).

The size structure of the population changed with station depth and season. Between May and November, the abundances of the three mysid length groups (<9, 9–15, and >15 mm) gradually became more closely aligned with station depth (Fig. 5). In spring, the densities of mysids ≤15 mm were homogeneous throughout the lake beyond the 50 m depth contour. However, the densities of mysids >15 mm increased significantly with station depth ($p < 0.001$) (Figs. 5, 6). In autumn, the abundance of the mysids <9 mm increased over the entire depth range, while the abundances of mysids 9–15 mm and >15 mm increased with station depth to 150 m (Figs. 5, 7).

Reproduction

More mature females carrying eggs occurred in the autumn than in the spring. In the autumn, the percentage of females carrying young and the mean size of females were similar at all depths beyond 100 m (Table 2); however, females of the same size carried slightly more eggs at the deeper stations (Fig. 8). Although the percentages of females ≥17 mm and <17 mm were similar in all depth ranges >100 m, the percentage of egg-bearing females <17 mm was lower in the 100–150 m depth range (Table 2). In the 50–100 m depth range, reproduction was depressed. Females were smaller (one-way analysis of variance, $p = 0.016$) and a smaller percentage of them carried eggs.

The level of reproduction was low during the spring and the percentage of females carrying eggs was similar throughout the lake (Table 2). Although average female size appeared to be smaller in the 50–100 m depth range than at deeper stations, the difference was not significant. The many small mysids (<7 mm in length) present in November indicate that young were released during the summer months, presumably from these females (Fig. 7).

Fig. 3. Mysid density distribution throughout Lake Ontario in the spring and fall plotted as Voroni polygons generated by a GIS system.

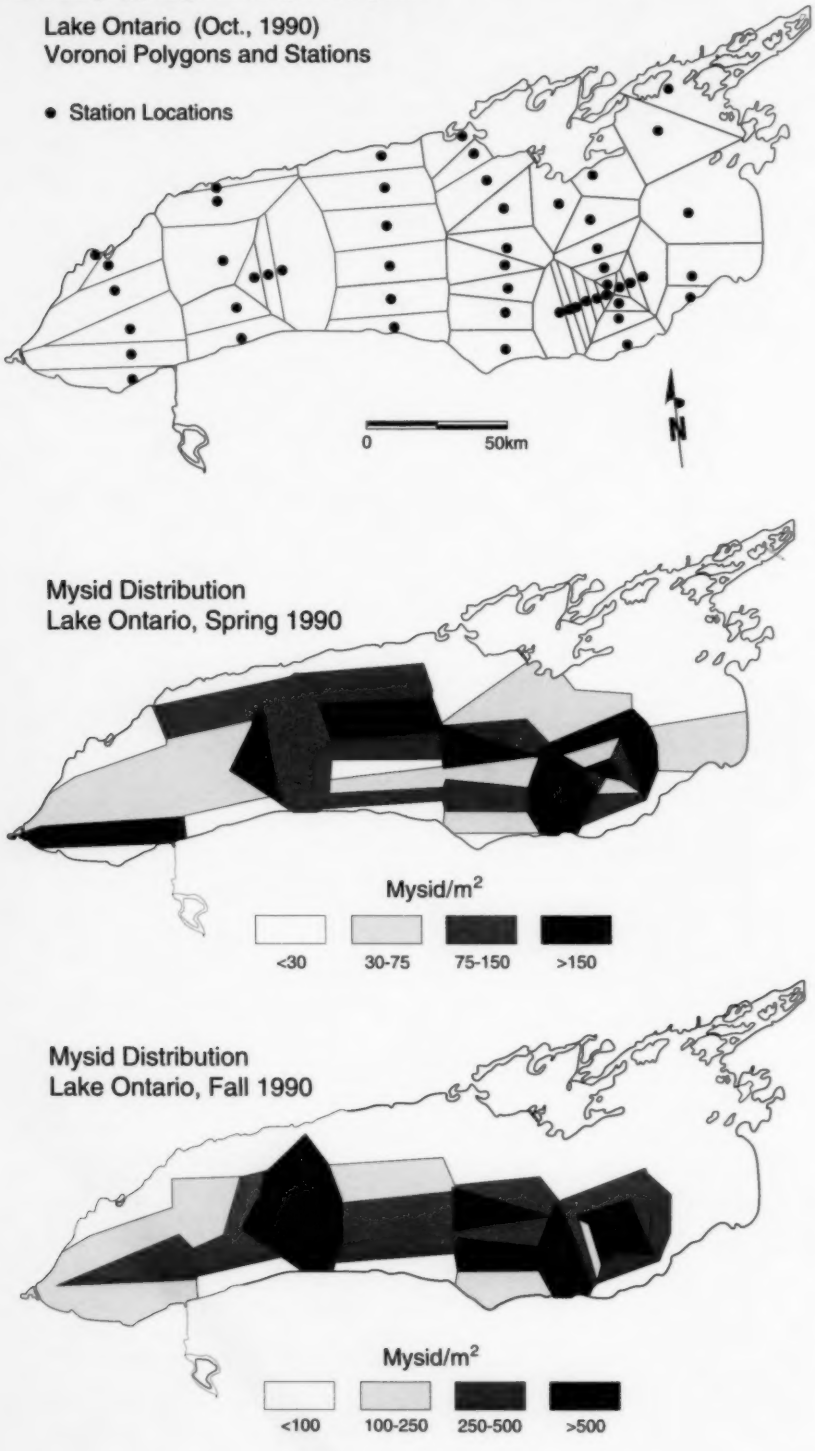


Fig. 4. Seasonal relationships between mysid density and station depth in Lake Ontario, 1990.

Spring:
20–100 m: log(density + 1) = 0.5384 + 0.014323(depth), $p = 0.034$, $r^2 = 30\%$;
≥100 m: log(density + 1) = 1.7367 + 0.002176(depth), ns.

Summer:
20–100 m: log(density + 1) = −0.1247 + 0.027251(depth), $p < 0.001$, $r^2 = 88\%$;
≥100 m: log(density + 1) = 2.8378 + 0.001722(depth), ns.

Autumn:
20–100 m: log(density + 1) = −0.3502 + 0.027933(depth), $p < 0.001$, $r^2 = 70\%$;
≥100 m: log(density + 1) = 1.96550 + 0.004196(depth), $p = 0.001$, $r^2 = 48\%$.

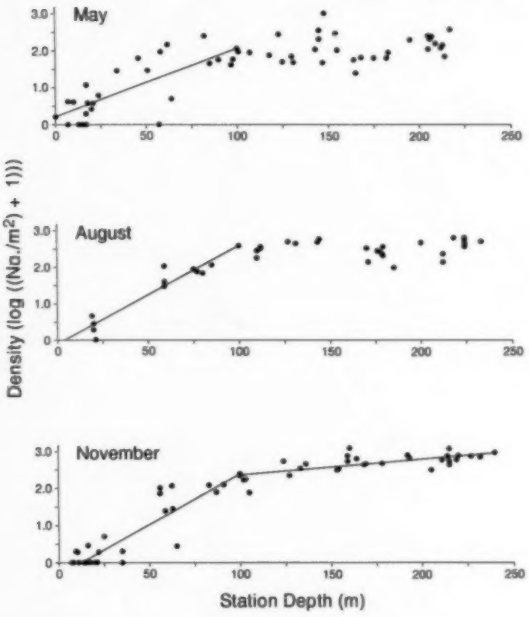
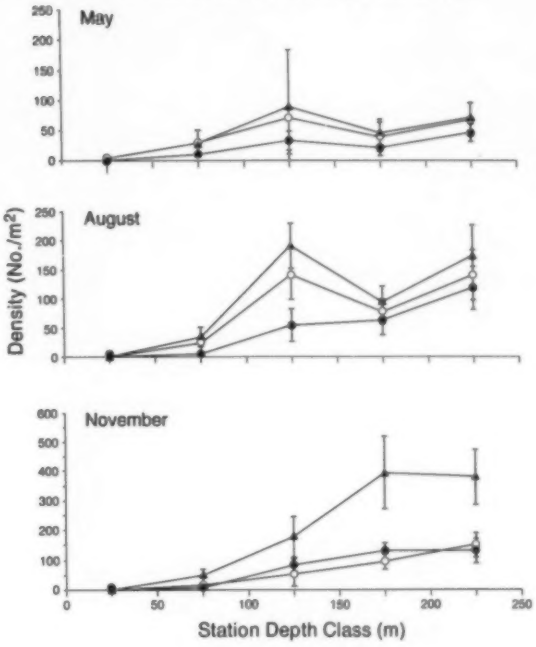


Fig. 5. Changes in mysid density across 50 m depth classes of sampling stations in Lake Ontario, 1990. Values are given as the mean ± 2 SE. ○, <9 mm in length, ▲, 9–15 mm in length, ●, >15 mm in length.



Growth rates

Peaks in size-class abundance from all depth ranges corresponded well with derived growth patterns for a spring and summer generation on the basis of growth rates in Johannsson (1992) (Fig. 9, Table 3). Summer reproduction was assumed to be centred in early August because an August cohort has been suggested for Lake Michigan (Morgan and Beeton 1978). Growth of the spring generation was faster between November and May than expected, but within the 1984–1987 range of growth patterns observed by Johannsson (1992, cf. Fig. 5). Therefore, Johannsson's (1992) average growth rates, and P_e/P_a and CPI values were used in the production calculations.

The addition of more recent length–weight data for mysids in Lake Ontario changed Johannsson's equation slightly. I used the following relationship to calculate the W_j values for the production equations:

$$\ln(\text{weight}) = -12.27 + 2.72 \ln(\text{length})$$

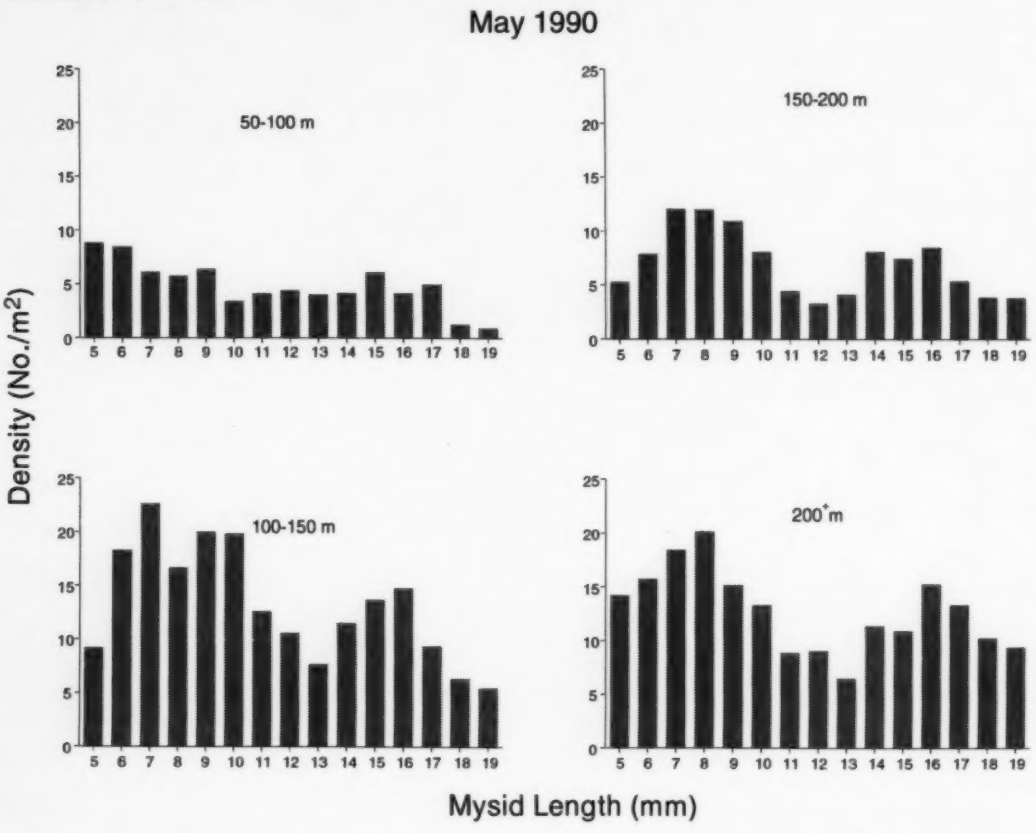
where weight is in grams, length is in millimetres. Length was measured from the tip of the rostrum to the cleft of the telson.

Production

Because mysid abundance and size-frequency distribution varied with station depth and not with location within the lake per se, production was calculated within each of the five depth ranges. Production estimates for the individual depth ranges were obtained by multiplying areal production estimates (in m^2) by the area between depth contours. Whole-lake production is the sum of the areal production estimates.

In this study, the abundance estimates for the lake did not balance across the seasons: more mysids 9–15 mm in length were observed in August than could be accounted for in the May samples, and more mysids ≥16 mm in length were observed in the 150–200 m depth range in November than could be accounted for in the August samples (Tables 4 and 5). Migration from the 100–150 m depth range could account for the increase in 9–12 mm mysids at station depths >150 m in November. I modified the abundance estimates of the 7–12 mm mysids in the May samples beyond

Fig. 6. Size-frequency distributions of mysids within four depth classes of sampling stations in Lake Ontario from the spring of 1990.



100 m depth so that the May and August abundances balanced, because the mysids must have been present but not sampled. This increased production estimates by 1.8–4.5%. The August abundance estimates of large mysids were not changed to match November abundances as only one depth range was affected.

Total annual production of mysids for the whole lake was 412.91×10^8 g dry weight·yr^{-1}. The annual rate of production increased from 0.02 g dry weight·m^{-2}·yr^{-1} in the nearshore (0–50 m) to 5.96 g dry weight·m^{-2}·yr^{-1} in the ≥200 m depth range, with rates much reduced at depths less than 100 m (Table 6). The greatest areal production occurred in the 100–150 m and 150–200 m depth ranges where higher rates of productivity occurred over large areas of the lake (Table 6).

The rate of production at station 41, which lies within the 100–150 m depth range, was 3.95 g dry weight·m^{-2}·yr^{-1} in 1990, similar to the lake-wide rate of 3.71 g dry weight·m^{-2}·yr^{-1}.

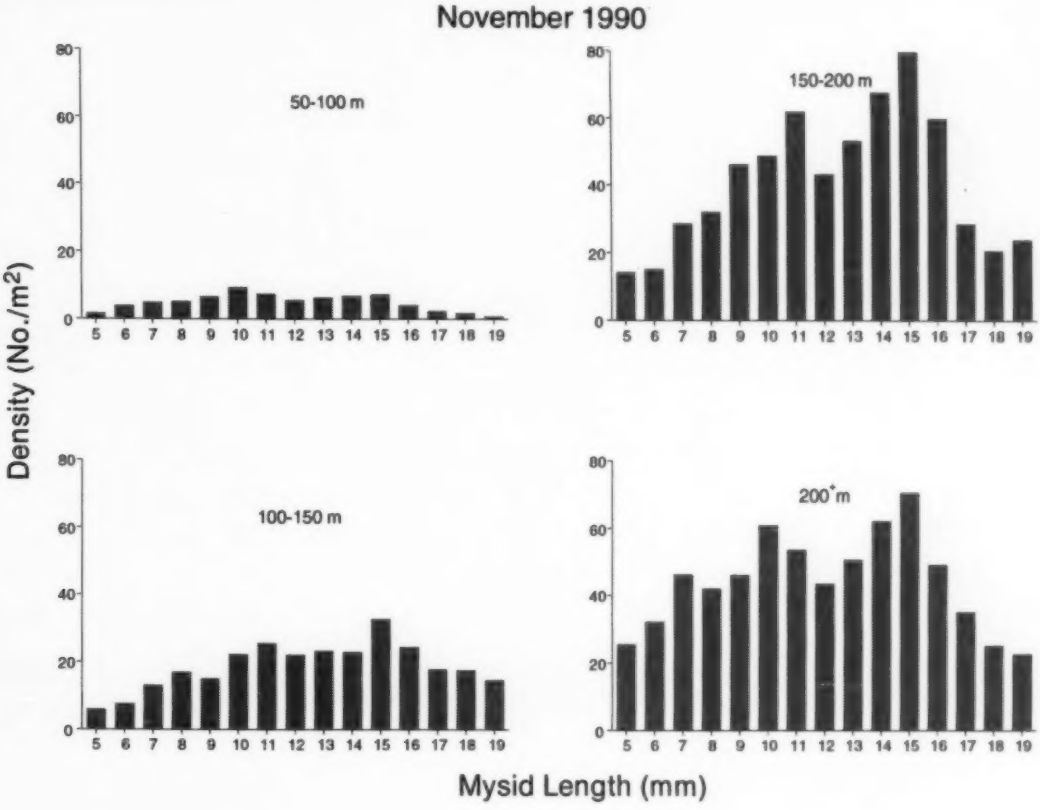
Discussion

Johannsson (1992) recognized that mysid size-frequency distributions and densities varied within Lake Ontario and that geographic regions with similar population structure needed to be delineated before mysid production could be calculated for the whole lake or portions of the lake. In the present study, I found that depth was the dominant spatial correlate with mysid abundance, population structure, reproductive status, and hence productivity. It should be noted that the deeper regions of the lake are not coincident with the centre of the lake, and therefore the relationships are more with depth, per se, than with distance from shore.

Patterns of production, and the underlying patterns of size distribution and density of the population, reflect the effects of a number of factors, such as predation, immigration–emigration, food supply, competition, habitat preference, and physical disturbance. At depths <100 m, the mysid population in Lake Ontario exhibited signs of predation and (or) emigration, i.e., the rapid increase in mysid density with depth between 20 and 100 m and the tightening of this relationship between May and November, the lower proportion of mysids >15 mm in length at depths <100 m than at depths >100 m, and the smaller size of females and proportion of mature females carrying eggs at depths <100 m than at depths >100 m.

The seasonal distributions and diets of fish suggest that predation on mysids may have been particularly intense

Fig. 7. Size-frequency distributions of mysids within four depth classes of sampling stations in Lake Ontario from the autumn of 1990.



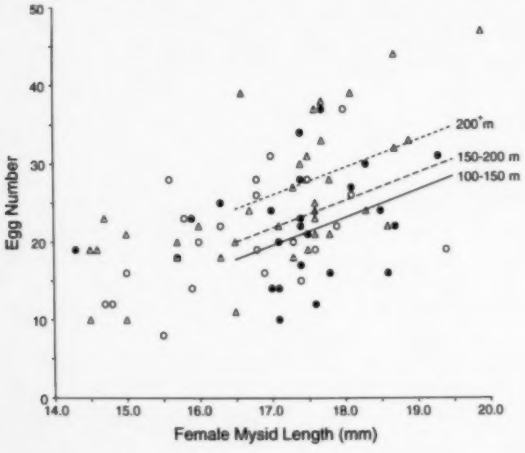
at depths <100 m and increased toward shore. These predators would include alewife, rainbow smelt (*Osmerus mordax*), and slimy sculpin (Morsell and Norden 1968; Janssen and Brandt 1980; Brandt 1986; Evans and Loftus 1987; Kjellberg et al. 1991; Mills et al. 1992). Alewife, the most abundant of these species, winter offshore at depths of 35–110 m and move inshore in April, following the bottom into shallow water (O'Gorman et al. 1987; Bergstedt and O'Gorman 1989). During this migration they feed on mysids as well as on zooplankton (Mills et al. 1992). In May, planktivorous fish occur throughout the water column to depths of 50–60 m with dense inshore, near-bottom aggregations near the shore (Schneider and Schaner 1992). Therefore, planktivore distribution in the spring is a mirror image of the May abundance gradient of mysids >15 mm in length.

Most information on summer planktivore distributions (smelt and alewife) comes from a series of experimental and whole-lake acoustical and midwater trawl surveys conducted by the Ontario Ministry of Natural Resources and the New York Department of Environmental Conservation between 1989 and 1992 (Schaner et al. 1989, 1991; Mathers et al. 1990, 1991; Schaner and Mathers 1990; Schneider and Schaner 1992). Planktivore densities were lower offshore (>100 m depth) than nearshore (<100 m depth). In the region <100 m in depth, higher densities of fish were observed inshore with fish distributions extending to the bottom out to depths of 50–75 m. Older smelt were usually densest in the metalimnion or hypolimnion, giving them access to mysids. Older alewife were more abundant in the epilimnion in the June–July samples in 1989 and 1992, a distribution similar to that observed in gill nets by Olson et al. (1988). During June and July, the bulk of the alewife population was separated from the mysid population by strong thermal barriers, and the diet of alewife in July contained only zooplankton, no mysids (Mills et al. 1992). In the mid-July to mid-August trawls in 1991 the older alewife were found predominantly in the metalimnion. Alewife gained access to mysids as the thermal barriers weakened through the summer and autumn: by October mysids were an important component of their diet (Mills et al. 1992). Slimy sculpins, which inhabit the lake bottom at depths <100 m, also fed heavily on mysids (Brandt 1986). Given these planktivore distributions, higher mortality rates should be suffered by mysids toward shore at depths <100 m, and in the nearshore (<100 m depth) than in the offshore (>100 m depth).

Table 2. Measures of the reproductive status of the mysid population living within 50 m depth ranges in Lake Ontario in the spring and fall of 1990.

Season	Depth range (m)	Percentage of population with young (mean ± SD)	Percentage of females carrying young	Ratio of females with embryos	Female size (mm) (mean ± SE)	Percentage of females ≥17 mm in length	Percentage of egg-bearing females ≤16.9 mm in length
May	50–100	0.45±1.15	4.6 (3/65)	1/3	16.39±0.17	29	100
	100–150	0.21±0.48	1.7 (3/175)	2/3	16.78±0.12	41	100
	150–200	0.68±1.04	5.6 (6/107)	2/6	16.85±0.18	41	33
	≥200	0.38±0.60	2.2 (4/180)	2/4	16.85±0.14	42	50
November	50–100	0.42±0.99	3.6 (3/82)	0/3	16.10±0.16	29	0
	100–150	4.80±4.53	21.5 (34/158)	10/34	16.83±0.14	48	14
	150–200	2.34±2.98	12.1 (34/280)	10/34	16.60±0.10	41	57
	≥200	4.10±2.63	23.5 (48/204)	12/51	16.62±0.10	43	39

Fig. 8. Relationships between the number of eggs produced and size of female mysids in the autumn of 1990 in Lake Ontario. ●, 100–150 m; ○, 150–200 m; △, ≥200 m. Covariance analysis was restricted to individuals >16.5 mm in length because few females smaller than this size carried eggs in the 100–150 m depth range. The mean size was 17.7 mm, the common slope was 3.5449, and adjusted mean egg numbers were 21.99, 24.20, and 28.42 for increasing depth ranges.



Emigration of mysids from the nearshore may have been partly responsible for the observed gradients. Although none of the decreases in mysid abundances in the 50–100 m depth range were significant, evidence for migration of mysids from shallower to deeper regions was seen in the 100 to >200 m depth range (Tables 4 and 5). It is likely that the trend extended into shallower areas but that densities were too low and too variable there to reveal it.

No evidence was found for a gradient in size-selective predation beyond 100 m depth. The mean size of mature females, the proportion of mature females ≥17 mm in length and the proportion of females carrying eggs were

Table 3. Comparison of the mean cohort lengths (mm) derived from knowledge of growth rates and times of birth (Fig. 9) and peaks in size-frequency distributions derived for the lake within 50 m depth ranges in 1990 (Figs. 6, 7).

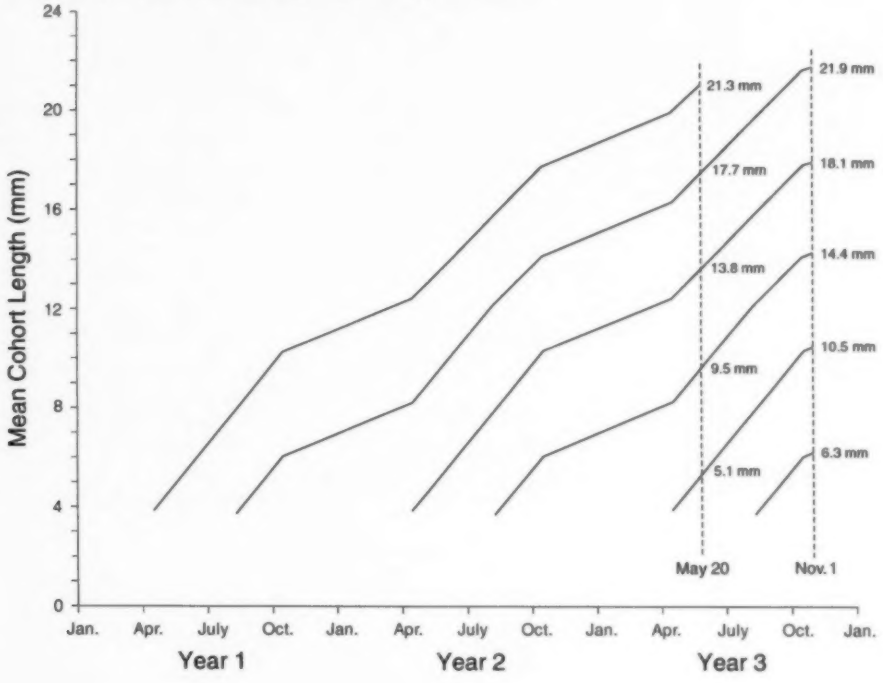
	Cohort				
	1	2	3	4	5
May 20					
Mean cohort length (Fig. 9)	21.3	17.7	13.8	9.5	5.1
Observed peaks (Fig. 6)					
50–100 m		17.0	15.0	7–9	5–6
100–150 m			14–16	9–10	6–7
150–200 m			14–16	7–9	P[a]
≥200 m		16–17	14–15	7–8	P[a]
November 1					
Mean cohort length (Fig. 9)	21.9	18.1	14.4	10.5	6.3
Observed peaks (Fig. 7)					
50–100 m			14–15	10	
100–150 m			15–16	11	8
150–200 m			14–16	9–11	P[a]
≥200 m			14–15	10–11	7

[a]Present in abundance but no clear peak.

similar from 100 to ≥200 m. Few fish inhabit the offshore waters of Lake Ontario. The deepwater sculpin, which preyed on *Diporeia* spp. and mysids, is now extinct. Small populations of whitefish and lake trout, whose young feed on benthic invertebrates, inhabit the hypolimnion. Alewife densities were lower offshore than nearshore (acoustical surveys discussed above) and alewife only feed on mysids in early spring and through the late summer and autumn (Mills et al. 1992). The increase in mysid density with depth in the autumn beyond 100 m may have more to do with offshore migrations (Table 5) and more successful production of summer young with depth (Fig. 10) than with any pattern of predation.

The mean brood size of a standard-sized female mysid increases as lake productivity or food supply increases

Fig. 9. Mysid population size structure derived from the combination of March and August generations with overlapping cohorts. Growth rates were taken from Johannsson (1992): 1st summer, 0.035 mm·d^{-1}; winter, 0.012 mm·d^{-1}; 2nd summer, 0.029 mm·d^{-1}. Expected mean cohort lengths on the LOTT sampling dates are extracted.



(Morgan 1980; Beeton and Gannon 1991). In the present study, females carried more eggs as station depth increased and started reproducing at a smaller size beyond 150 m depth (cf. Table 2, Fig. 8). However, growth rates during the first year of life were similar throughout the lake. As juvenile mysids tend to optimize growth rates and not the accumulation of lipids (Adare 1992), these observations indicate that only the nutrition of larger mysids improved with depth. How the nutrition of larger mysids was improved is not known. They may have had more time to feed in the water column on high-quality food at deeper stations. Alternatively, they may have spent less time hiding from predators and more time feeding, or expended less energy avoiding predators at deeper stations than at shallower stations. In Lake Ontario, the potential for mysid production appears to increase with depth as the density of predators decreases and the nutrition of reproductive individuals increases.

Mysids in deeper regions of the lake may act as a reservoir and support predation nearer shore through winter redistribution. If we accept that the distributions and abundances of mysids in spring and fall 1990 in Lake Ontario are typical, then the seasonal maps of mysid abundance provide pictorial evidence of winter movement of mysids in the lake, particularly from the region of the deep trench, in the southeast, toward the northwest and west (Fig. 3). The greater patchiness in spring than in autumn and the breakdown in abundance – station depth relationships of mysids ≤15 mm in length over the winter further support this hypothesis (Figs. 5, 10).

It is often difficult to determine whether changes in density are the result of dispersal or variable mortality rates. In this instance, no obvious source of mortality would act over the winter on both the newly hatched and older mysids to create this patchy distribution. On the other hand, there is an obvious means of dispersal: translocation of mysids by strong hypolimnetic currents. Mass movements of mysids by upwelling currents have been reported by Reynolds and DeGraeve (1972), Shea and Makarewizc (1989), and Johannsson (1992). Immigration of mysids into the region of the Bioindex station in July 1985 and October 1987 was thought to have resulted from upwelling events created by strong northwest winds. Winds out of the northwest set up surface currents running from the northwest to the southeast, and return currents moving from the southeast to the northwest in the deeper waters (Simons and Schwertzer 1987). The deep currents would be swung further west as they encounter the Coriolis currents that broadly circle the perimeter of the lake. These return currents would carry vertically migrating mysids to the northwest and west. Therefore, a seasonal cycle of redistribution appears to exist with density–depth gradients developing over the summer through migration and mortality and weakening over the winter through the action of storms and currents.

Table 4. Net changes in mysid densities within depth ranges between May and August 1990.

Size ranges used in May and August (mm)	Depth range (m)	Mean density (No./m^2)			Area of depth range ($m^2 \times 10^3$)	Density difference (No. $\times 10^8$)	Probability of difference
		May	August	Difference			
May: 7.0–10.9	50–100	21.7	19.7	−2.0	43.28	−86.5	ns
Aug.: 9.0–12.9	100–150	79.2	130.0	50.8	43.92	2231.1	0.0025
	150–200	43.0	62.0	19.0	32.56	618.6	ns
	≥200	67.0	99.5	32.5	5.44	176.8	ns
May: 11.0–13.9	50–100	12.4	11.9	−0.6	43.28	−26.0	ns
Aug.: 13.0–15.9	100–150	30.9	61.0	30.1	43.92	1322.0	0.0002
	150–200	11.8	33.4	21.6	32.56	703.3	0.0053
	≥200	24.5	52.4	27.9	5.44	151.8	0.0001
May: ≥14.0	50–100	21.4	6.6	−14.8	43.28	−640.5	ns
Aug.: ≥16.0	100–150	61.2	54.4	−6.8	43.92	−298.7	ns
	150–200	37.1	63.6	26.5	32.56	862.8	ns
	≥200	70.5	111.0	40.5	5.44	220.3	ns

Note: Growth during that period would be approximately 2 mm. Significance of differences was determined by applying a *t* test or median test, as appropriate.

Table 5. Net changes in mysid densities within depth ranges between August and November 1990.

Size ranges used in August and November (mm)	Depth range (m)	Mean density (No./m^2)			Area of depth range ($m^2 \times 10^3$)	Density difference (No. $\times 10^8$)	Probability of difference
		August	November	Difference			
Aug.: 6.0–9.9	50–100	33.2	28.8	−4.4	43.28	−190.4	ns
Nov.: 9.0–12.9	100–150	172.4	85.2	−87.2	43.92	−3829.8	0.0115
	150–200	79.2	200.0	120.8	32.56	3933.2	0.0643[a]
	≥200	107.2	204.4	97.2	5.44	528.7	0.0004
Aug.: 10.0–12.9	50–100	28.0	20.4	−7.6	43.28	−326.8	ns
Nov.: 13.0–15.9	100–150	144.1	79.2	−64.9	43.92	−2850.4	0.0045
	150–200	78.2	200.7	122.5	32.56	3989.9	0.0160[a]
	≥200	128.3	183.6	55.3	5.44	300.8	ns
Aug.: ≥16.0	50–100	6.6	8.9	2.3	43.28	99.5	ns
Nov.: ≥16.0	100–150	54.6	74.8	20.2	43.92	887.2	ns
	150–200	63.6	133.1	69.5	32.56	2262.9	0.0015
	≥200	112.2	132.4	20.2	5.44	109.9	ns

Note: It was assumed that once mysids reached the 13.0–15.9 mm size-class they remained in that size-class until they reproduced in November. Therefore, the August abundances for this size-class consist of animals in the 13.0–15.9 mm size-class plus those that would grow into that size-class by November.

[a]This value is based on medians, not means, owing to one high value. If this value is removed, *p* decreases.

The objectives of the present study were to define spatial patterns in mysid production, to relate them to the biological and physical structure of the Lake Ontario ecosystem, and to provide production estimates for whole-lake tropho-dynamic models. Although the spatial pattern of mysid production is clear, production itself may be underestimated by approximately 20%. Because samples were not collected evenly and frequently throughout the year, the production estimates are biased toward those size-classes present during the sampling period. Examination of cohort size through sequential years indicates that the greatest loss of biomass in the population (and hence accumulation of production) occurred after the animals reached 13–15 mm in length (Johannsson 1992; O.E. Johannsson, unpublished results). Production of the spring cohort was well estimated because it grew through the 14- to 18-mm size-classes between May and November. Production of summer mysids was not well estimated because they passed through the 14- to 18-mm size-classes over the winter and early spring (Fig. 9). Johannsson et al. (1994) estimated that 93% of newborns belonged to the spring generation at the Bioindex station, 41. Therefore, production was likely underestimated by approximately 7% in the 100–150 m depth range, and to some degree in other regions of the lake. The production estimates were further underestimated by approximately 13% because the data were

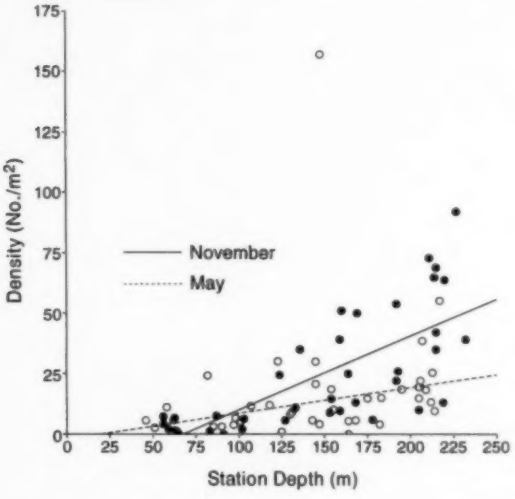
Table 6. Annual production of *Mysis relicta* in Lake Ontario in 1990 broken down by depth ranges.

Depth range (m)	Lake surface area ($m^2 \times 10^8$)	Production[a] (g dry weight·m^{-2}·yr^{-1})	Areal production[a] (10^8 g dry weight·yr^{-1})
0–50	59.61	0.02±0.01 (0.02)	1.37±0.69 (1.68)
50–100	43.28	0.91±0.18 (1.12)	39.38±7.79 (48.44)
100–150	43.92	3.71±0.37 (4.56)	162.94±16.25 (200.39)
150–200	32.56	5.43±0.44 (6.68)	176.80±13.72 (217.44)
≥200	5.44	5.96±0.87 (7.33)	32.42±4.71 (39.87)
Lake total	184.81		412.91±43.16 (506.82)

Note: Whole-lake production was 412.91±43.16 × 10^8 g dry weight·yr^{-1} (mean ± SD).

[a]Production estimates modified for a net efficiency of 87% and an underestimation of the August generation productivity by approximately 7% (see text) are presented in parentheses. These values may still underestimate productivity (see text).

Fig. 10. Relationship between the distribution of summer newborns and station depth in the autumn (≤6.5 mm in length in November) (●) and spring (8.5–10.0 mm in length in May) (○). The lines are significantly different (slopes, $p = 0.0014$; means, $p = 0.0034$). November: density = −20.82 + 0.3067(depth) ($p < 0.0001$). May: density = −2.09 + 0.1062(depth) ($p = 0.002$), one outlier at 146 m removed.



not corrected for net efficiency. Production, corrected for these losses, is given in parentheses in Table 6.

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References

Adare, K.I. 1992. Seasonal changes in the total lipid content and life cycle characteristics of the freshwater shrimp, *Mysis relicta*. M.Sc. thesis, Trent University, Peterborough, Ont.

Balcer, M.D., N.L. Korda, and S.I. Dodson. 1984. Zooplankton of the Great Lakes. A guide to the identification and ecology of the common crustacean species. The University of Wisconsin Press, Madison, Wis.

Beeton, A.M., and J.E. Gannon. 1991. Effect of environment on reproduction and growth of *Mysis relicta*. Am. Fish. Soc. Symp. 9: 144–148.

Bergstedt, R.A., and R. O'Gorman. 1989. Distribution of alewives in south-eastern Lake Ontario in autumn and winter: a clue to winter mortalities. Trans. Am. Fish. Soc. 118: 687–692.

Bowers, J.A., W.E. Cooper, and D.J. Hall. 1990. Midwater and epibenthic behaviours of *Mysis relicta* Loven: observations from the Johnson-Sea-Link II submersible in Lake Superior and from a remotely operated vehicle in northern Lake Michigan. J. Plankton Res. 12: 1279–1286.

Brandt, S.B. 1986. Ontogenetic shifts in habitat, diet, and diel-feeding periodicity of slimy sculpin in Lake Ontario. Trans. Am. Fish. Soc. 115: 711–715.

Carpenter, G.F., E.L. Mansey, and N.H.F. Watson. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319–325.

Evans, D.O., and D.H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by rainbow smelt, *Osmerus mordax*: their freshwater niche and effects on indigenous fishes. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 249–266.

Grossnickle, N.E. 1982. Feeding habits of *Mysis relicta*: an overview. Hydrobiologia, 93: 101–107.

Grossnickle, N.E., and M.D. Morgan. 1979. Density estimates of *Mysis relicta* in Lake Michigan. J. Fish. Res. Board Can. 36: 694–698.

Iversen, T.M., and P. Dall. 1989. The effect of growth pattern, sampling interval and number of size classes on benthic invertebrate production estimated by the size-frequency method. Freshwater Biol. 22: 323–332.

Janssen, J., and S.B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37: 177–184.

Johannsson, O.E. 1992. Life history and productivity of *Mysis relicta* in Lake Ontario. J. Great Lakes Res. 18: 154–168.

Johannsson, O.E., L.G. Rudstam, and D.C. Lasenby. 1994. *Mysis relicta*: assessment of metalimnetic feeding and implications for competition with fish in lakes Ontario and Michigan. Can. J. Fish. Aquat. Sci. 51: 2591–2602.

Kjellberg, G., D.O. Hessen, and J.P. Nilssen. 1991. Life history, growth, and production of *Mysis relicta* in the large, fiord-type Lake Mjosa, Norway. Freshwater Biol. 26: 165–173.

Lasenby, D.C., and M. Furst. 1981. Feeding of *Mysis relicta* Loven on macrozooplankton. Inst. Freshwater Res. Drottningholm Rep. 59: 75–80.

Lasenby, D.C., and R.R. Langford. 1973. Feeding and assimilation of *Mysis relicta*. Limnol. Oceanogr. 18: 280–285.

Lasenby, D.C., T.G. Northcote, and M. Furst. 1986. Theory, practice, and effects of *Mysis relicta* introductions to North American and Scandanavian lakes. Can. J. Fish. Aquat. Sci. 43: 1277–1284.

Mathers, A., T. Schaner, and C.P. Schneider. 1990. Alewife and smelt catches in midwater trawls during the 1990 survey of Lake Ontario. Chap. 9. 1990 Annual Report. Lake Ontario Fisheries Unit, Ontario Ministry of Natural Resources, Picton, Ont.

Mathers, A., T.J. Stewart, and A. Goyke. 1991. Alewife and smelt abundance estimates from midwater beam trawls and hydroacoustic surveys in Canadian waters of Lake Ontario, 1991. Chap. 13. 1991 Annual Report. Lake Ontario Fisheries Unit, Ontario Ministry of Natural Resources, Picton, Ont.

McDonald, M.E., L.B. Crowder, and S.B. Brandt. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. Limnol. Oceanogr. 35: 220–227.

McWilliam, P.S. 1970. Seasonal changes in abundance and reproduction in the opossum shrimp *Mysis relicta* Loven in Lake Michigan. M.Sc. thesis, University of Sydney, Sydney, Australia.

Menzies, C.A. 1980. A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. 25: 770–773.

Mills, E.L., R. O'Gorman, J. DeGisis, R.F. Heberger, and R.A. House. 1992. Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. Can. J. Fish. Aquat. Sci. 49: 2009–2019.

Moen, V., and A. Langeland. 1989. Diurnal vertical and seasonal horizontal distribution patterns of *Mysis relicta* in a large Norwegian lake. J. Plankton Res. 11: 729–745.

Morgan, M.D. 1980. Life history characteristics of two introduced populations of *Mysis relicta*. Ecology, 61: 551–561.

Morgan, M.D., and A.M. Beeton. 1978. Life history and abundance of *Mysis relicta* in Lake Michigan. J. Fish. Res. Board Can. 35: 1165–1170.

Morgan, M.D., and S.T. Threlkeld. 1982. Size dependent horizontal migration of *Mysis relicta*. Hydrobiologia, 93: 63–68.

Morgan, M.D., S.T. Threlkeld, and C.R. Goldman. 1978. Impact of the introduction of kokanee and opossum shrimp on a subalpine lake. J. Fish. Res. Board Can. 35: 1572–1579.

Morsell, J.W., and C.R. Norden. 1968. Food habits of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proc. 11th Conf. Gt. Lakes Res. pp. 96–102.

Mostellar, F., and J.W. Tukey. 1977. Data analysis and regression: a second course in statistics. Addison-Wesley Publishing Company, London.

Naesje, T.F., B. Jonsson, L. Klyve, and O.T. Sandlund. 1987. Food and growth of age-0 smelts, *Osmerus eperlanus*, in a Norwegian fjord lake. J. Fish Biol. 30: 119–126.

Nero, R.W. 1982. A description of three nets suitable for estimating the abundance of *Mysis relicta*. Can. Tech. Rep. Fish. Aquat. Sci. 1046: iv + 8 p.

Nero, R.W., and I.J. Davies. 1982. Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Can. J. Fish. Aquat. Sci. 39: 349–355.

Nero, R.W., and W.G. Sprules. 1986. Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (Malacostraca: Mysidacea). Can. J. Fish. Aquat. Sci. 43: 420–434.

O'Gorman, R., R.A. Bergstedt, and T.H. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44: 390–403.

Olson, R.A., J.D. Winter, D.C. Nettles, and J.M. Haynes. 1988. Resource partitioning in summer by salmonids in south-central Lake Ontario. Trans. Am. Fish. Soc. 117: 552–559.

Parker, J.I. 1980. Predation by *Mysis relicta* on *Pontoporeia hoyi*: a food chain link of potential importance in the Great Lakes. J. Great Lakes Res. 6: 164–166.

Reynolds, J.B., and G.M. DeGraeve. 1972. Seasonal population characteristics of the opossum shrimp, *Mysis relicta* in southern Lake Michigan. Proc. 15th Conf. Great Lakes Res. pp. 117–131.

Salemaa, H., K. Tyystjarvi-Muuronen, and E. Aro. 1986. Life histories, distribution and abundance on *Mysis mixta* and *Mysis relicta* in the northern Baltic Sea. Ophelia, 4: 239–247.

Schaner, T., and R.A. Mathers. 1990. Lake Ontario hydroacoustic survey for alewife and smelt. Chap. 15. Lake Ontario Fisheries Unit. 1990 Annual Report. Ontario Ministry of Natural Resources, Picton, Ont.

Schaner, T., R.A. Mathers, T.H. Eckert, and C.P. Schneider. 1989. Community Oriented Lake Assessment Program, 1989. Chap. 9. Lake Ontario Fisheries Unit. 1989 Annual Report. Ontario Ministry of Natural Resources, Picton, Ont.

Schaner, T., C.P. Schneider, and J.N. Bowlby. 1991. Hydroacoustic surveys of Lake Ontario, 1991. A progress report. Chap. 12. Lake Ontario Fisheries Unit, 1991 Annual Report. Ontario Ministry of Natural Resources, Picton, Ont.

Schneider, C.P., and T. Schaner. 1992. Pelagic prey stocks in Lake Ontario, 1991–1992. Chap. 16. Lake Ontario Fisheries Unit. 1992 Annual Report. Ontario Ministry of Natural Resources, Picton, Ont.

Sell, D.W. 1982. Size-frequency estimates of secondary production by *Mysis relicta* in lakes Michigan and Huron. Hydrobiologia, 93: 69–78.

Shea, M.A., and J.C. Makarewicz. 1989. Production, biomass and trophic interactions of *Mysis relicta* in Lake Ontario. J. Great Lakes Res. 15: 223–232.

Simons, T.J., and W.M. Schwertzer. 1987. Stratification, currents and upwelling in Lake Ontario, summer 1982. Can. J. Fish. Aquat. Sci. 44: 2047–2058.

Sokal, R.R., and F.H. Rohlf. 1969. Biometry. W.H. Freeman and Co., San Francisco.

Estimation of historical stock sizes and recruitment anomalies from relative abundance time series

Carl Walters

Abstract: Often only simple relative abundance time series and basic growth and (or) survival estimates are available for assessing impacts of fishing and environmental factors. Assessment then involves fitting production models to the series, while forcing the model with observed catch or effort series. A key uncertainty in this approach is how to deal with recruitment variations due to factors other than stock size. A dynamic programming algorithm can be used to compute maximum likelihood estimates of the recruitment anomaly sequence, given prior knowledge of growth parameters, the natural survival rate, and proportion of the variation in the relative abundance index that is due to abundance measurement errors. The temporal pattern of anomaly estimates from the dynamic programming procedure is quite robust to uncertainties about the absolute stock size and average historical recruitment rate, so it can at least provide information for studies of factors affecting recruitment in cases where the abundance index measurement error is small compared with recruitment process errors (<10% of total error). Further, the procedure can easily be embedded within a Bayesian or maximum likelihood estimation of stock size and surplus production.

Résumé : On ne dispose souvent que de simples séries chronologiques sur l'abondance relative et d'estimations rudimentaires de la croissance et de la survie pour évaluer les impacts de la pêche et des facteurs environnementaux. L'évaluation consiste alors à ajuster les modèles de production aux séries chronologiques et à forcer le modèle en y intégrant les séries de données sur les prises observées ou l'effort. Une des principales causes d'incertitude de cette approche est la façon de traiter les variations du recrutement dues à des facteurs autres que la taille du stock. Or, on peut se servir d'un algorithme de programmation dynamique pour calculer des estimations à probabilité maximale de la séquence des anomalies de recrutement, si on dispose de données antérieures sur les paramètres de croissance, le taux naturel de survie et la proportion de la variation de l'indice d'abondance relative qui est due aux erreurs de mesure de l'abondance. Le profil temporel des estimations d'anomalie obtenues par programmation dynamique est peu affecté par les incertitudes concernant la taille absolue du stock et le taux historique moyen de recrutement, de sorte qu'il peut au moins apporter de l'information sur les facteurs qui touchent le recrutement dans les cas où l'erreur de mesure de l'indice d'abondance est faible par rapport aux erreurs reliées au recrutement (<10% de l'erreur totale). En outre, la procédure peut facilement être enchâssée dans une estimation bayésienne, ou à probabilité maximale, de la taille du stock et de la production excédentaire.
[Traduit par la Rédaction]

Introduction

There is a long history in fisheries assessment of using relatively simple production models to obtain estimates of stock size and sustainable yield when only overall catch and relative abundance data are available. The essential concept underlying these methods is of a generalized "depletion estimator": We examine how much impact various known absolute removals (catches) have had on relative abundance in the past, while trying at the same time to account for or estimate the effects of natural production processes (recruitment, growth, survival) on relative abundance. This is a most ambitious undertaking, and it is not surprising that we often cannot decide whether the data came from a large, unproductive stock or a small, productive one; this uncertainty is expressed in large variances of, and strong correlation among, the production and stock size parameter estimates. We most often do the estimation using an "observation error" approach first articulated clearly by Pella (1967; Pella and Tomlinson 1969). The removal and production effects are described by a deterministic model, and we seek production and stock size parameter estimates that make the time series predictions from this model fit the observed time series as closely as possible (for reviews of recent applications, see Polacheck et al. 1993; Prager 1994). It has been shown that this approach should often give good parameter estimates even when there is substantial "process error" resulting from biological production variations not accounted for in the

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deterministic model (especially "environmental" effects on recruitment) and, in fact, assuming only such process error effects can lead to badly biased parameter estimates (Hilborn and Walters 1992; Polacheck et al. 1993). Attempts to deal with both observation and process errors simultaneously (e.g., Ludwig et al. 1988; Ludwig and Walters 1989) have led to complicated algorithms that do not appear to improve much on simpler procedures.

There is a need for production model fitting procedures that not only account for various realistic combinations of process and observation error effects but also extract as much information as possible from the relative abundance time series about the historical pattern of process effects, especially recruitment "anomalies." These patterns can tell us much about why and how a simple production model may be failing and could be directly useful in fisheries oceanography studies aimed at uncovering effects of various environmental factors on recruitment. Further, combined or mixed error-fitting procedures should generally provide more realistic assessments of uncertainty than do the observation error methods that have recently become more popular (Walters and Ludwig 1994); observation error procedures can give dangerously optimistic assessments of uncertainty, while process error procedures can give assessments that are unnecessarily conservative (Walters 1986).

This paper proposes a simple dynamic programming algorithm for calculating maximum likelihood estimates of recruitment-anomaly sequences (historical recruitment patterns) from relative abundance time-series and catch data. This algorithm is computationally more efficient than general nonlinear search procedures for long data series, and guarantees to find the globally best estimates. It is assumed that the analyst has available a "reliable" abundance index that has on average been proportional to actual stock size (if the index is catch per unit effort (CPUE), it should not display hyperdepletion, hyperstability, or temporal trends in catchability as defined in Hilborn and Walters 1992) with an unknown proportionality constant, that total removals from this population (catches) have been measured accurately, and that natural mortality and growth parameters are known. In the best case, there should also be an auxiliary time series of average body sizes caught in both the catch and abundance indexing procedure, so that the time series can be converted to numbers of fish if the original units are biomass.

The following sections first develop the procedure, then show how it performs with both simulated and real data series for which there are independent recruitment anomaly estimates from age-composition data. A final section discusses its use in broader assessment frameworks including the Bayesian assessment approach suggested by Walters and Ludwig (1994).

Dynamic programming procedure for estimating recruitment anomalies

Suppose the data available for assessment are time series of catches C_t, $t = 1, 2, \ldots, n$, relative abundances y_t, and possibly average body weights in the catch, W_t. Assume further that independent estimates are available of the annual natural survival rate $S = \exp(-M)$ and the Ford–Brody growth parameters α, ρ, and W_k (slope and intercept of the Walford plot of weight at age $a + 1$ versus weight at age a, and body weight W_k at entry to the harvested population; growth parameters needed only if the catch and abundance index data are in biomass units). Then ignoring age-dependent variation in survival rate and time-dependent changes in growth rate, population biomass B_t can be predicted over time from the Deriso–Schnute relationship (Deriso 1980; Schnute 1985; see derivation in Hilborn and Walters 1992, pp. 331–336):

$$[1] \quad B_{t+1} = g_t B_t + W_k R \exp(w_{t+1})$$

where R is the mean number of animals recruiting to the vulnerable population per year and w_{t+1} is a lognormal "recruitment anomaly" for year $t + 1$. Note that total recruits $R\exp(w_{t+1})$ entering the population each year need not represent a single cohort or year-class (Schnute 1985); a strong cohort that recruits over several years would produce a sequence of anomalies reflecting the "mesh selection" pattern. The growth–survival factor, g_t, is given by

$$[2] \quad g_t = S(1 - C_t/B_t)\,[\alpha/\overline{W}_t + \rho]$$

(g_t reduces to just $S(1 - C_t/B_t)$, the total survival rate of fish already present in year t, if the catch and relative abundance data are in numbers units; in that case, also set $W_k = 1$). Alternative production models besides Eqs. 1 and 2 can be used in the derivation below; the only necessary requirement is that the production or recruitment anomaly w_{t+1} be represent explicitly so that a conditional calculation of it can be made for any given combination of B_t, B_{t+1}. For the above model, this conditional calculation is just

$$[3] \quad w_{t+1} = \log[(B_{t+1} - g_t B_t)/(RW_k)]$$

Note in the above equations that historical harvest rates C_t/B_t enter the assessment via the g_t term; again, the only general requirement is that the production model explicitly represent the effects of C_t on biomasses B_t.

Note also that Eq. 1 assumes no stock–recruit relationship, i.e., there are assumed to be strong compensatory mechanisms that result in average recruitment R no matter how low B may be. This is an absurd and dangerous assumption from a management perspective (no possibility of recruitment overfishing). But as noted below, the estimation of w_t under this "null" assumption can provide a simple way of checking for recruitment overfishing (as a correlation between calculated ws and Bs).

Assume that the abundance index y_t has been measured so as to satisfy the additive measurement error:

$$[4a] \quad y_t = qB_t + v_t$$

or the lognormal measurement error

$$[4b] \quad y_t = qB_t \exp(v_t)$$

where the abundance indexing or catchability parameter q is unknown. Note that such proportional abundance indices are hard to come by in fisheries work and generally require the use of research surveys and (or) careful spatial analysis of catch rate data; raw CPUE data generally contain effects of temporal and density-dependent changes

in q caused by technology development and nonrandom searching by fishermen.

Using the above definitions and relationships, we can now pose the following conditional estimation problem. For fixed R and q (i.e., conditional on R and q), what sequence of biomass estimates B_t will maximize the normal likelihood function $L(y)$:

$$[5] \quad L(y) = K\exp\{-0.5\Sigma v_t^2/\sigma_v^2 - 0.5\Sigma w_t^2/\sigma_w^2\}$$

(where K is an integration constant) or, equivalently, minimize the variance-weighted sum of squares:

$$[6] \quad S(y) = \Sigma v_t^2/\sigma_v^2 + \Sigma w_t^2/\sigma_w^2$$

The separate observation σ_v^2 and process σ_w^2 variances can be eliminated from the sums of squares minimization by making some prior assumption about the variance ratio $V = \sigma_v^2/\sigma_w^2$. Given an assumed value for this V, the maximum likelihood sequence B_t is that which minimizes

$$[7] \quad S(y,V) = \Sigma v_t^2 + V \Sigma w_t^2$$

A useful way to think about V is as a measure of prior belief in the proposition that recruitment anomalies have been a stationary, independent sequence of random effects. Low values of V (e.g., 0.001–0.1) represent low confidence in this assumption, while high values of V force S to be minimized at a solution sequence B_t very near to the deterministic prediction of Eq. 1. In setting up procedures to minimize S, it is useful to note that as V approaches zero (no observation error, S consists only of squared recruitment anomalies), the maximum likelihood estimates of the w's conditional on q and R move to the limiting values given by assuming $B_t = y_t/q$ in Eq. 3:

$$[8] \quad w_{t+1} = \log\left(\frac{y_{t+1}/q - g_t y_t/q}{W_k R}\right) \qquad \text{if } V = 0$$

This equation can be used to obtain a quick feeling for the apparent pattern of recruitment anomalies over time, provided q is low enough that the apparent exploitation rate $1 - C_t/(y_t/q)$ is greater than zero; the more elaborate procedures described below generally give a qualitatively similar pattern (spikes, trends) of w estimates but with absolute values decreasing as V increases. Note that changing the absolute average recruitment R in Eq. 8 causes only an additive shift in the anomaly estimates; this property holds approximately for the elaborate procedures as well and is why qualitative assessments of the anomaly pattern are not dependent on having good estimates of overall stock size or recruitment. Note further that Eq. 8 has the same basic differencing structure ($y_t - ry_{t-1}$) used in two-stage regression procedures to correct for effects of autocorrelation in data (e.g., see Anderson and Wilen 1985; Walters 1990); in this case, the differencing structure is accounting for autocorrelations created by persistent effects of recruitment anomalies on population size.

Two approaches can be used to seek the sequence w_2, w_3, ..., w_n that minimizes S in Eq. 6 or 7. The most obvious is to treat the ws as parameters in a nonlinear search procedure; such searches can now be implemented very quickly using spreadsheet functions such as Microsoft Excel's Solver. This search will usually require at least 10 n^2 calculations of the terms in Eq. 1 (i.e., 10 nonlinear search iterations with n^2 1-year-ahead predictions at each iteration), and is not guaranteed to find a unique maximum likelihood solution.

The second approach is to use a dynamic programming procedure as suggested by Larson and Casti (1982). As described in the Appendix, this procedure typically requires on order of 300n calculations of Eq. 1 (i.e., is numerically more efficient than nonlinear search for long data series, $n >$ 30 years), and guarantees to find the global maximum likelihood estimates of the w's. The basis of this procedure is simply to express the sum of squares S as a recursive relationship $S_t = v_t^2 + Vw_t^2 + S_{t+1}$ where S_t is the sum of squares from time t forward to time n, then solve the following local minimization problem backward in time ($t = n - 1$, $n - 2$, ..., 1):

$$[9] \quad S_t^*(B_t) = \min_{B_{t+1}}[v_t^2 + Vw_{t+1}^2 + S_{t+1}^*(B_{t+1})]$$

where $S_t^*(B_t)$ is the minimum of S_t for each possible value B_t of the optimum state estimate at time t. Note that performing this minimization for each possible B_t results in a conditional optimum estimate of the function $B_{t+1}^*(B_t)$, i.e., B_{t+1}^* is the value of B_{t+1} that minimizes the bracketed expression in Eq. 9 once B_t has been fixed (for each possible B_t, B_{t+1}, v_t and w_{t+1} are calculated by Eqs. 3 and 4). The optimum state estimate and corresponding w sequence is then found by starting with that value of B_1 that minimizes S_1^*, and for each successive time ($t = 2, 3, \ldots, n$) just "reading off" the next stored value of $B_{t+1}^*(B_t)$.

Measures of statistical error for the anomaly estimates should be calculated only in cases where the analyst is confident that the assumed value of V is correct. In such cases, standard errors for the w_t conditional on q, R, and V can be obtained by treating the w's as fixed, unknown parameters (Schnute 1994), then applying various methods for approximating parameter uncertainty in nonlinear estimation. The simplest approach here is to use a standard covariance approximation:

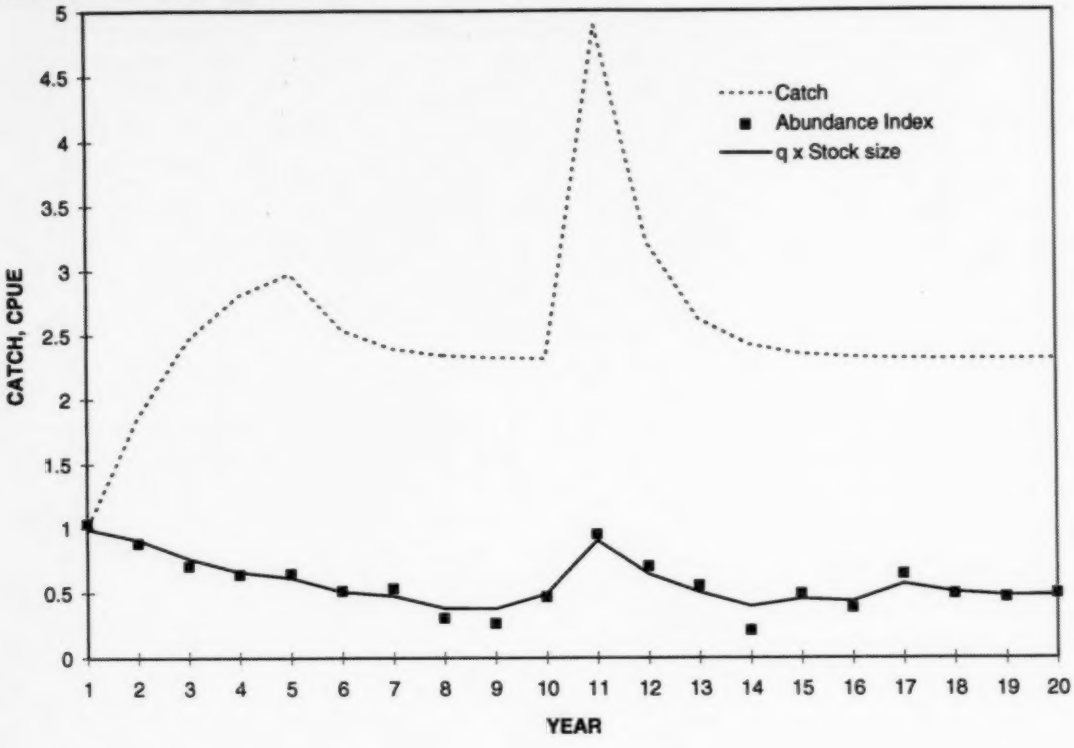
$$[10] \quad \text{var}(w_t) = \sigma_v^2(\mathbf{J}'\mathbf{J})_{tt}^{-1}/(qRW_k)^2$$

where tt denotes the t, t element of the approximate information matrix $(\mathbf{J}'\mathbf{J})^{-1}/(qRW_k)^2$ and $\mathbf{J}$ is the Jacobian (sensitivity) matrix $\partial y_t/\partial w_t$ after factoring out the constant factor qRW_k:

$$[11] \quad \begin{aligned} \mathbf{J}_{ij} &= 0, && \text{if } i < j \\ &= \exp(w_i), && \text{if } i = j \\ &= \mathbf{J}_{i-1,j}g'_{j-1}, && \text{if } i > j \end{aligned}$$

Here, g'_j is the reduced survival–growth effect $s[\alpha/W_j + \rho]$ and represents how the sensitivity of the predictions to each w drops off over time. The matrix $(\mathbf{J}'\mathbf{J})^{-1}$ is close to tridiagonal (exactly so for constant g'), indicating that only adjacent w estimates are correlated; under the null hypothesis $w = 0$, the i, i element of this matrix is just $1 + g'^2$ and the t, $t + 1$ covariance element is just $-g'$. That is, under the null hypothesis $w = 0$ for all t, the estimates w_t will vary randomly with approximate standard deviation $\sigma_v(1+g'^2)^{1/2}/(qRW_k)$. However, I urge great caution in the use of such approximations for power analysis and for deciding whether particular anomaly estimates are

Fig. 1. Simulated catch, biomass, and relative abundance index for a test population subject to a single strong recruitment anomaly (positive) in year 10.



"significant," since the results are entirely dependent on using known V to estimate σ_v from the model residuals. If V is truly unknown, there are no error degrees of freedom for estimating σ_v, i.e., for distinguishing between recruitment anomaly and observation error effects.

A particularly useful extension of the basic algorithm may be to embed it within a line search for the maximum likelihood (minimum S) estimate of q. Then the resulting maximum likelihoods can be used to plot likelihood profiles for R and (or) the unfished biomass $B_o = W_k R/(1 - g_o)$, and the minimum sums of squares from time 1 forward (S^* recorded from step 3 above) can be used in the formulae of Walters and Ludwig (1994) to provide Bayes posterior probability distributions for these parameters integrated over q and over the measurement variance (see below).

Tests of the procedure on simulated data with extreme recruitment anomaly patterns

Simulated data were generated for the difficult "one way trip" (Hilborn and Walters 1992) assessment situation where exploitation rate increases linearly over time (from 0.1 to 0.6) then stabilizes. Annual natural survival s (or natural growth–survival parameter) was set to 0.5, so that recruitment anomaly effects for the single spike and random cases defined below would not be too easy to detect (i.e., so that each anomaly would not have very persistent and obvious effects on abundance); this represents the relatively favorable situation of having either direct data on numbers caught or accurate estimates of average body weight in the catch for each year. Measurement errors (v) were assumed to have a coefficient of variation of 0.1, fairly typical of the unexplained variation around deterministic production model fits to actual relative abundance time series. Then, recruitment to this simulated population was driven with five recruitment anomaly patterns (w_t sequences) that represent roughly the range of patterns seen in recruitment anomalies for actual populations: (1) random, lognormal, independent over time; (2) a single, large positive anomaly in year 5; (3) a sinusoidal pattern with period 7 years; (4) a linear decreasing trend over time (from $w_1 = 1$ to $w_{20} = -1$); and (5) a decreasing trend caused by making simulated recruitment a Beverton–Holt function of spawning biomass (recruitment overfishing case). Of particular interest is case 5, where the issue is whether the methodology can detect recruitment overfishing even when the basic estimation model (Eq. 1) does not admit this possibility.

Figure 1 shows a typical catch, abundance, and abundance index time series from one of the simulations (single anomaly case), to show that the simulated time series are not unlike patterns seen in many developing fisheries.

Fig. 2. Comparison of simulated recruitment anomaly patterns with maximum likelihood estimates of these patterns obtained with the dynamic programming algorithm. Simulated time-series data were similar to example in Fig. 1 except in relation to timing and pattern of recruitment anomaly effects. Error bars for selected years show approximate standard errors for anomaly estimates, estimated by Eq. 10.

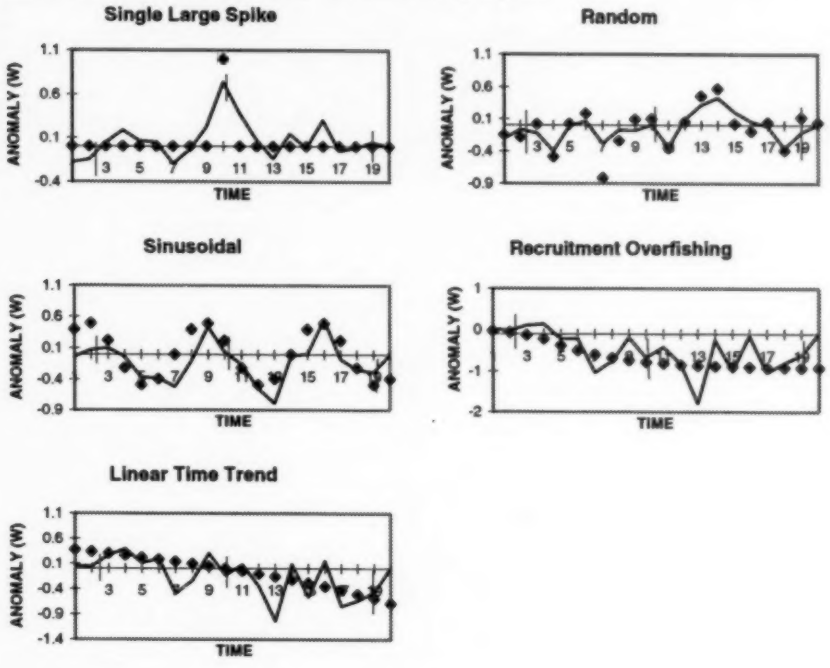


Figure 2 shows performance, again from typical simulation trials, of the algorithm for the various w_t sequence cases. The reconstructed w_t estimates shown in Fig. 2 are those evaluated at the maximum likelihood estimates of R and q and for $V = 0.1$; a similar qualitative pattern over time is obtained for a wide range of R values, provided the results are displayed at the most likely q value for each R. Increasing R causes the mean anomaly to decrease (the whole sequence shifts from positive to negative while maintaining scale of variation), while increasing V causes the estimated sequence to be smaller and flatter (all estimated values decrease and move toward 0.0 as V increases).

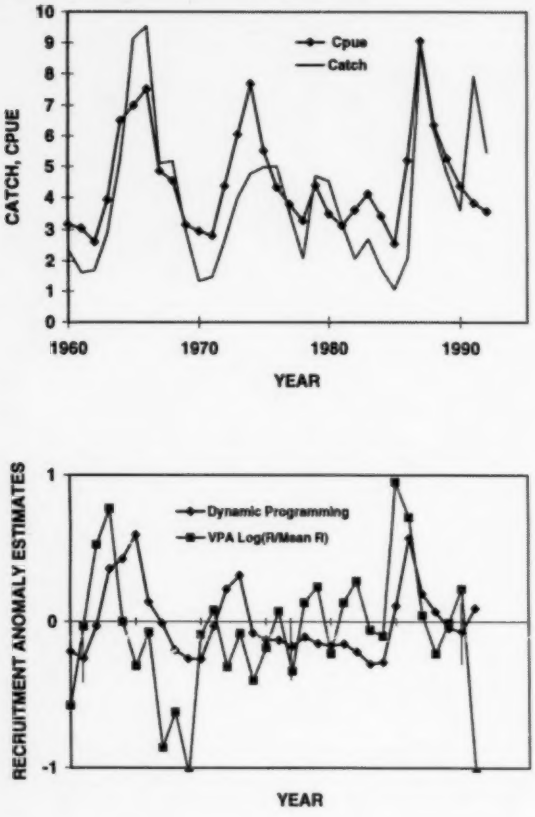
It is clear from Fig. 2 that the algorithm can recover at least the qualitative pattern of recruitment anomalies for cases where the anomalies are strongly patterned in time (cycle). The results for trend, as well as random and single-spike anomalies are less convincing; in these cases, the maximum likelihood estimates of w_t appear visually to be more strongly "contaminated" by measurement error effects. The largest anomalies are still visible, but the minimization of S results in incorrectly large w_t values for years when measurement errors v_t are large. This problem is not corrected by increasing V (assuming more of the variation is due to observation errors); such correction instead causes downward bias in the estimates of the larger w_t anomalies. Likewise, reducing V results in more of the measurement (v) effects appearing as spurious w_t estimates. The recruitment trend cases only appear to be well estimated because the correct trend line is presented with the estimates.

Examples with actual data series

It is difficult to find real data series where the $y = qB$ assumption is not badly violated. In the following examples, the y data are commercial CPUEs and, hence, must be viewed with great suspicion. These examples represent the sort of situations where the estimation method described above might help to complement other assessment methods or provide insight that might otherwise be missed.

Figure 3 shows calculated recruitment anomalies for Pacific cod (*Gadus macrocephalus*) in the Hecate Strait, British Columbia, and compares these with a recruitment time series estimated from length frequency data using the MULTIFAN system (Fournier et al. 1990). Data for this assessment were provided by M. Stocker, Pacific Biological Station, Nanaimo, B.C.; the CPUE and catch data can be found in Stocker and Hand (1993). s is assumed to be 0.5. An interesting feature of this population series is that CPUE and catch data indicate the occurrence of at least one strong year-class around 1973–1975, yet recruitment reconstructions based on length frequencies have failed to detect this obvious anomaly. Analyses of species interactions (Walters et al. 1986) and comparisons with a nearby

Fig. 3. Maximum likelihood estimates of recruitment anomalies for Pacific cod, Hecate Strait, British Columbia, based on the catch and CPUE data shown, compared with recruitment pattern estimated from length–frequency data using MULTIFAN. Error bars for selected years show approximate standard errors for anomaly estimates, estimated by Eq. 10.



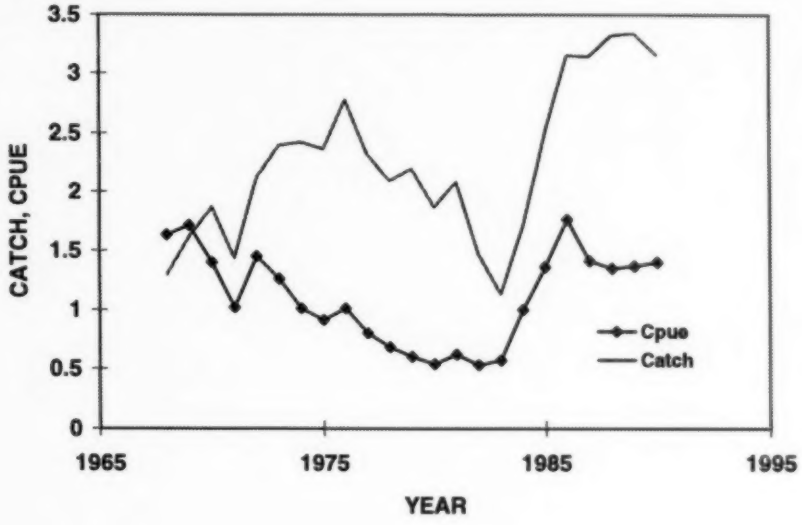
Vancouver Island stock also suggest that a strong anomaly should have occurred during the mid-1970s. So now we can conclude that either there indeed was such an anomaly and something unusual happened to growth rates during that period to make the strong year-class(es) invisible in terms of the length frequencies used to estimate age compositions for VPA, or else there was some major change in catchabilities (e.g., targeting on older age-classes) that made the CPUE and catch data nonrepresentative of abundance during the period. In this case the recruitment anomaly estimation has helped to define precise directions for further analysis of the historical data.

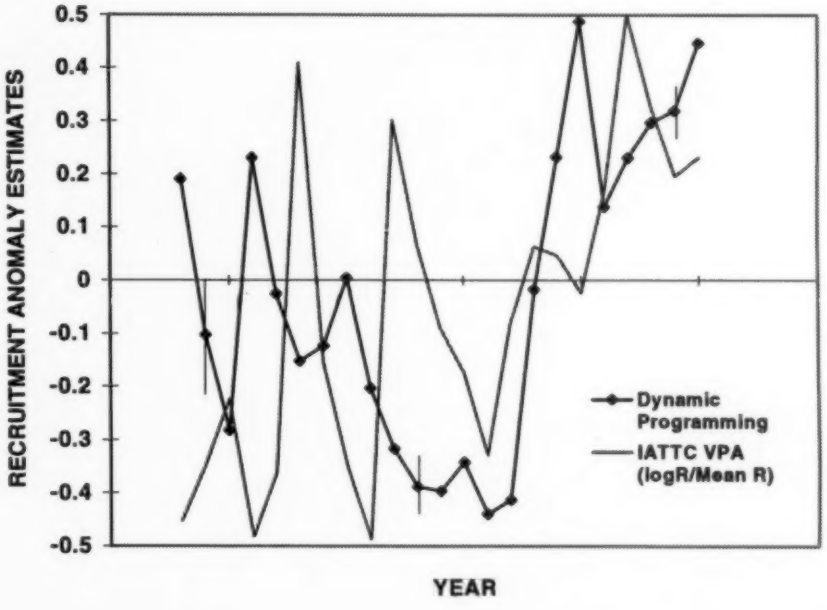
Figure 4 compares estimated recruitment anomalies with recruitment estimates based on length–frequency data for yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Data for this analysis are from IATTC (1992). s is assumed to be 0.6. Recruitment estimates are for the combined November (X) and May (Y) cohorts as defined by IATTC (1992, Table 22). As in the Pacific cod example, the estimated recruitment anomalies indicate stronger variation in year-class strength than is suggested by length–frequency data. IATTC staff have noted that the apparent positive recruitment anomalies after the early 1980s cannot be explained by any simple, deterministic production model; there has been a basic change in catchability and (or) extensions in the range of fishing to increase the effective stock size. A disturbing feature of this example is that the recruitment anomalies are positively correlated with the dynamic programming estimates of stock size the year before (Fig. 5; $R^2 = 0.41$, $P < 0.001$), implying a possible risk of recruitment overfishing. (This possibility is in fact implicit in the production models that have historically been used in management of this stock.) It is also worrisome that strong recruitment anomalies as evidenced by the CPUE and catch data appear to consistently lead the occurrence of strong year-classes in the IATTC assessment by 2 years; the IATTC year-class strengths are reported to be for the years when the fish reach 30 cm length, and it does not make sense to assume that these fish actually recruited to the fishery 2 years earlier.

Figure 6 shows a history of catches, CPUE, and calculated recruitment anomalies for American shad (*Alosa sapidissima*) of the Hudson River, New York. Here CPUE is only a very crude abundance index, equal to catch divided by the number of licensed gillnet fishermen (catch and license data provided by K. Hattala and A. Kahnle, New York Department of Conservation, Albany, N.Y.). In this example no long-term age-composition data are available for recruitment assessment, but there is much interest in assessing possible impacts of power plant entrainment and impingement; shad larvae have been impacted by a power plant near Albany since the early 1950s and, perhaps, by nuclear power plants since the early 1970s. A controversial issue in the Hudson River situation is whether strong compensatory mechanisms (stock–recruit relationships) act to reduce power plant impacts (Fletcher and Deriso 1988); such mechanisms should be relatively less important for stocks that have been overfished or otherwise reduced to the point where recruitment has been impaired or for which density-dependence is concentrated in early life stages that are still subject to entrainment. Density dependence has been demonstrated for such early stages in shad (Savoy and Crecco 1988) but not for the Hudson River stock. The recruitment anomalies shown in Fig. 6 strongly suggest that the stock has indeed been subject to massive recruitment overfishing, perhaps exaggerated by entrainment effects since the early 1950s. Both the maximum likelihood biomass estimates and direct analysis of age-composition data (K. Hattala, personal communication) indicate that exploitation rates are still on the order of 50%/year, yet the stock is producing only a tiny fraction of the harvest that it produced under similar exploitation rates in the early 1950s (Talbot 1954). Further, the 1940–1960 harvest peak shown in Fig. 6 was preceded by an even higher peak in the late 1800s, which led to a collapse from which the stock was likely still recovering when the data series shown in Fig. 6 started.

Decline of the northern cod (*Gadus morhua*, NAFO 2J3KL) stock off Newfoundland from 1962 to 1977 was followed by a major Canadian initiative to rebuild the

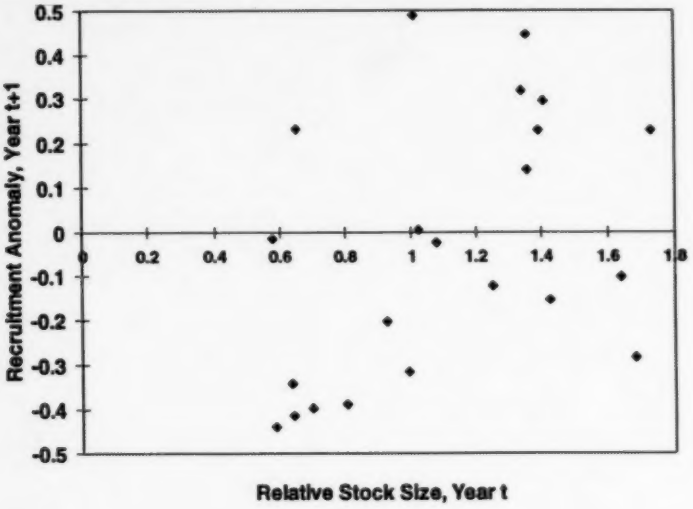
Fig. 4. Maximum likelihood estimates of recruitment anomalies for yellowfin tuna in the eastern tropical Pacific, based on the catch and CPUE data shown, compared with recruitment pattern estimated from size composition data and cohort analysis. Error bars for selected years show approximate standard errors for anomaly estimates, estimated by Eq. 10.





stock during the late 1970s and 1980s. Estimates of stock size and recovery rate turned out to be way too optimistic (Finlayson 1994; Hutchings and Myers 1994; Walters 1994), at least partly because recruitment rates were lower than expected and are apparently closely related to stock size. Virtual population analyses in the late 1970s did not reveal the recruitment decline (Myers et al. 1993), and an interesting question is whether the recruitment anomaly methodology of this paper would have detected it. To address this question, I "cheated" by constructing a relative abundance index from assessments in Hutchings and Myers (1994) showing that commercial CPUE has varied as about the 0.4 power of stock biomass (the index is CPUE divided by average weight of fish caught, raised to the 1/0.4 power;

Fig. 5. Relationship between estimated recruitment anomalies and estimated stock biomass the previous year, for the yellowfin tuna data shown in Fig. 4.



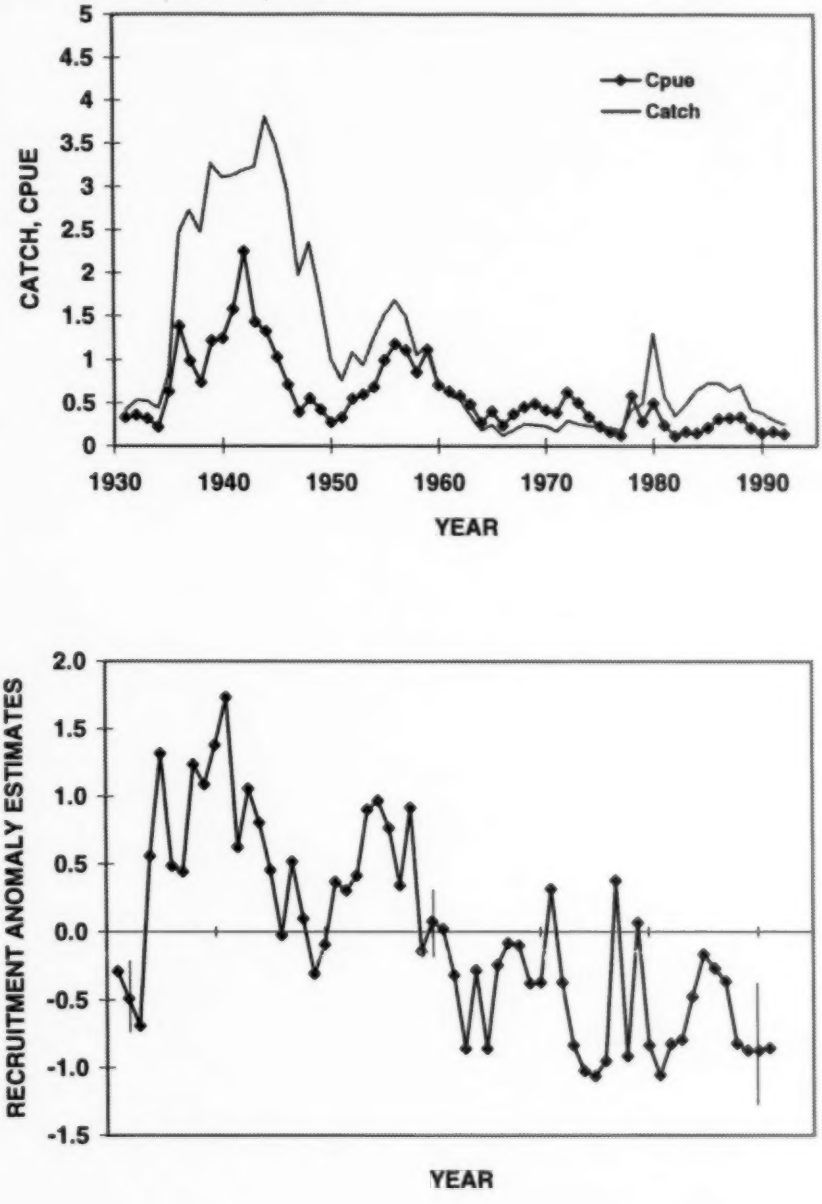
this index of numerical relative abundance should be about proportional on average to stock size); while such a correction for hyperstability in the abundance index could have been constructed from VPA and CPUE data available as of the late 1970s, it was not standard at that time to look for such effects in groundfish data. I then assumed $s = \exp(-0.2)$ and avoided g, corrections for growth by using catch in numbers (from Baird et al. 1991). The resulting recruitment anomaly estimates for $V = 0.01$ are compared with recruitment anomaly estimates from Baird et al. in Fig. 7. Two discrepancies between the "actual" anomalies based on VPA and the estimates from aggregate, corrected CPUE data are immediately obvious: (1) the aggregate data lead to smoothing of the anomaly sequence, likely representing how each individual year-class recruits to the harvestable stock over several years; and (2) as in the fake data tests, the severity of the recruitment decline (negative anomalies in recent years) is underestimated. So it would have provided some indication of impending recruitment decline, but this indication would not have been so strong as to have been taken very seriously in management planning.

Linking with broader assessments

Beyond providing maximum likelihood reconstructions of population biomass histories $B^*(t)$ conditional on R and q, the dynamic programming algorithm can be used in at least three further ways. First, it can be embedded in a numerical search procedure for the maximum likelihood estimates of R and q, thus providing an overall most likely biomass trajectory for the stock (including a best estimate of the current stock size $B^*(n)$). However, such point estimates can be very misleading, and a better option is to systematically vary at least R so as to construct a likelihood profile or Bayesian assessment as described below.

Second, it can be used as the first step in an iterative model-building process aimed at providing a functional description of how recruitment (estimated for each year as $R\exp(w_t)$) varies with stock size and with environmental factors. The basic concept here is to first examine the apparent anomaly sequence computed under the assumptions of constant average recruitment and independent random anomalies, then replace these assumptions with more realistic models for how (and when) the anomalies arise. This modelling is particularly important if the anomalies are obviously not independent (cycle, trend, etc.), since any Bayesian assessment of uncertainty about population parameters will not be valid (most likely will be too conservative) if it is based on a likelihood function that assumes independent errors. A key issue in this process is to decide whether there is evidence of recruitment overfishing, in the form of a positive relationship between recruitment and stock size at least for low stock sizes. For example, the Hudson River shad data (Fig. 6) suggest a saturating or Beverton–Holt form of stock–recruitment relationship for the average effect of stock size on recruitment, with the current stock size producing only about one third of the average recruitment rate that might be exhibited if the spawning stock were allowed to rebuild. However, note that regression analysis of the calculated recruitment rates and stock sizes should not be used to estimate stock–recruitment parameters for situations like the shad; errors-in-variables effects (Ludwig and Walters 1981; Walters and Ludwig 1981) and time series effects (especially with the strongly autocorrelated residuals apparent in Fig. 6; Walters 1990) would make such regressions highly suspect. A better approach when stock–recruitment effects

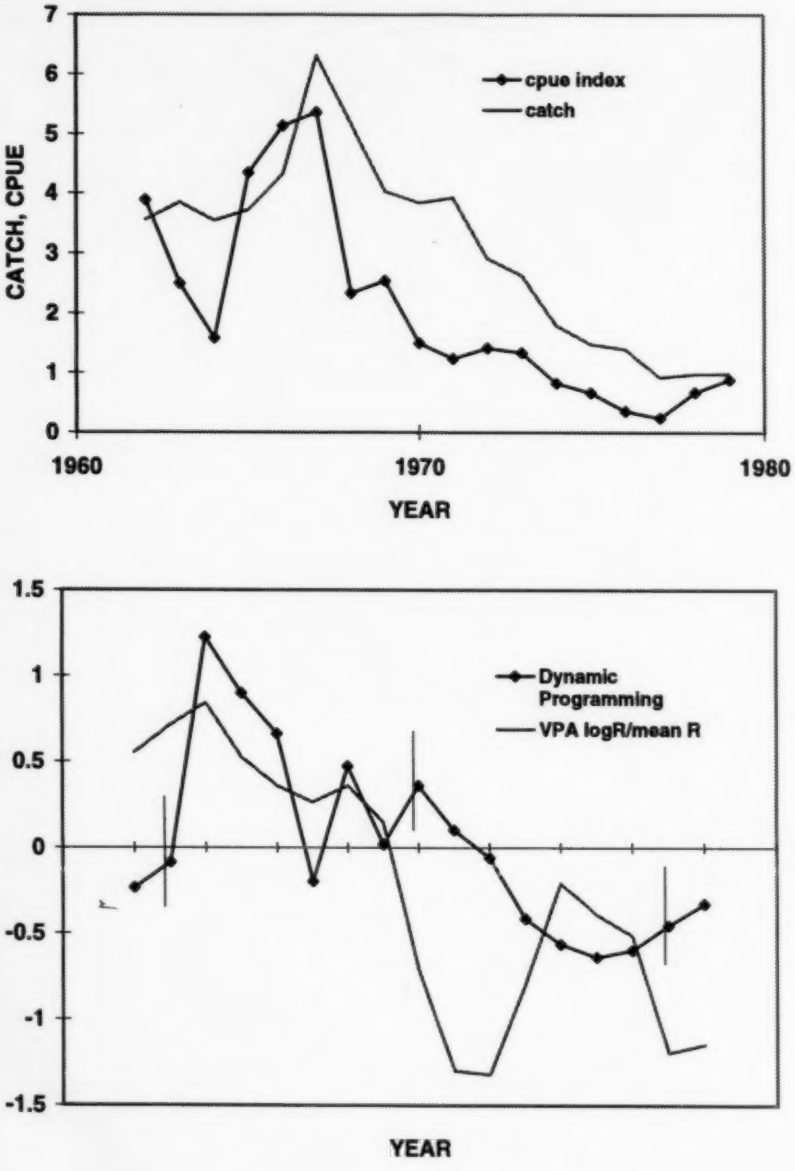
Fig. 6. Maximum likelihood estimates of recruitment anomalies for American shad in the Hudson River, based on catch and the crude CPUE index (catch/number of gillnet fishing licenses) shown. Error bars for selected years show approximate standard errors for anomaly estimates, estimated by Eq. 10.



may be important is to simply fit a production model with a recruitment relationship to the time series (replace R of Eq. 1 with an appropriate stock–recruit function, then use fitting procedures as reviewed in Hilborn and Walters 1992).

It is important not to expect too much from a stepwise procedure for recruitment model development. In most fisheries data series, environmental and stock size effects on recruitment are badly confounded (Walters and Collie 1988) so that it is logically impossible to decide whether stock size declines are due to environmental effects on recruitment or are instead directly causing recruitment to decline. In the shad example, are recruitments now low because of overfishing, or is stock size now low because

Fig. 7. Maximum likelihood estimates of recruitment anomalies for northern cod (NAFO 2J3KL) stock off Newfoundland, based on catch and CPUE index estimated from power relationship between commercial CPUE and VPA biomass estimates. Error bars for selected years show approximate standard errors for anomaly estimates, estimated by Eq. 10. Estimates are compared with anomalies from VPA based on data in Baird et al. (1991).



recruitment has been adversely impacted by factors such as power plant entrainment? The best that can be expected from an iterative model development procedure is to define a clear set of alternative hypotheses about causes of recruitment variation, for use in risk assessment and evaluation of experimental policy options.

Third, the S^* estimates can be used in assessment of Bayes posterior probabilities for "leading parameters" including R and $B(n)$. Following the derivations in Walters and Ludwig (1994), an approximate marginal-likelihood kernel integrated over q and the measurement error variance (σ_v^2) is given for any value of the leading parameters by

[12] $L^* = (S^*)^{-m} I^{-1/2}$

where $m = (n - 1)/2$ and $I = \sum B_t^{*2}$. This is not an exact marginal likelihood over q because the maximum likelihood estimates of w_t that form part of S^* are dependent on q, so $I^{-1/2}$ is not the exact integration factor for q. If L^* is computed for each value of R on a grid of values wide enough to contain all probable values of R, then the posterior probability for any R value on this grid is just its associated L^* divided by the sum of the L^* values over all grid points. A "binning procedure" as in Walters and Punt (1994) can be used to add up L^* values for bin ranges of B_n during this calculation, and each such sum divided by the total of L^* over the R grid points is an estimate of the posterior probability that B_n lies in the corresponding bin range. The grid of leading parameter values can be multidimensional (e.g., combinations of s and R instead of just R values), but it quickly becomes impractical to compute S^* at enough grid points to provide a satisfactory approximation to even the shape of the posterior distribution.

Simulation experiments (as in Figs. 1 and 2) on calculation of posterior probability distributions for R suggest that the posterior distribution mode (maximum likelihood estimate if no prior information, value of R that maximizes L^* in eq. 12) tends to be lower than the true value ("biased" downward) when V is assumed to be small (more process error, less observation error). This is similar to the bias toward underestimating stock size and overestimating productivity reported for process error estimation of production model parameters by other authors (Polacheck et al. 1993). Thus when the posterior distribution is to be used in harvest decision analyses, a safer strategy when V is unknown is to assume a large value for it; however, this strategy will result in underestimates of recruitment anomalies and, hence, should not be employed when the main objective of analysis is the study of recruitment patterns.

A key limitation of the dynamic programming algorithm is that it cannot be used to solve for S^* values for more general population models that replace R in Eq. 1 with a recruitment prediction based on past spawning biomass B_{t-k}, where k is the number of years from spawning to recruitment, unless $k = 1$ (recruits at $t + 1$ dependent on B_t). That formulation would allow representation of overfishing risk in terms of a leading parameter representing the slope of the recruitment curve at low stock sizes. A dynamic programming algorithm can be developed for such situations, but this algorithm would be much slower than direct search procedures for the maximum likelihood values of the w_t, and even direct search procedures would require massive computation when repeated at many points on a leading parameter grid.

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References

Anderson, J.L., and J.E. Wilen. 1985. Estimating the population dynamics of coho salmon (*Oncorhynchus kisutch*) using pooled time-series and cross-sectional data. Can. J. Fish. Aquat. Sci. 42: 459–467.

Baird, J.W., C.A. Bishop, and E.F. Murphy. 1991. An assessment of the cod stock in NAPO Divisions 2J3KL. CAFSAC Res. Doc. 91/53: 84 p.

Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Can. J. Fish. Aquat. Sci. 37: 268–282.

Finlayson, A. 1994. Fishing for truth: a sociological analysis of northern cod stock assessments from 1977–1990. Institute of Social and Economic Research, Memorial University, St. John's, Nfld. 176 p.

Fletcher, R.I., and R.B. Deriso. 1988. Fishing in dangerous waters: remarks on a controversial appeal to spawner–recruit theory for long-term impact assessment. Am. Fish. Soc. Monogr. 4: 232–244.

Fournier, D.A., J.R. Sibert, J. Majkowski, and J. Hampton. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tune (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47: 301–317.

Hilborn, R., and C. Walters. 1992. Quantitative fisheries stock assessment and management: choice, dynamics, and uncertainty. Chapman & Hall, New York, N.Y.

Hutchings, J.A., and R.A. Myers. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. 51: 2126–2146.

IATTC (Inter-American Tropical Tuna Association). 1992. Annual report for 1991. IATTC, La Jolla, Calif. 271 p.

Larson, R.E., and J.L. Casti. 1982. Principles of dynamic programming. Part II: advanced theory and applications. Marcel Dekker, Inc., New York Control Syst. Theory Ser. 7: 497 p.

Ludwig, D., and C. Walters. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. 38: 711–720.

Ludwig, D., and C. Walters. 1989. A robust method for parameter estimation from catch and effort data. Can. J. Fish. Aquat. Sci. 46: 137–144.

Ludwig, D., C. Walters, and J. Cooke. 1988. Comparison of two models and two estimation methods for catch and effort data. Nat. Resour. Modell. **2**: 457–498.

Myers, R.A., K.F. Drinkwater, N.J. Barrowman, and J.W. Baird. 1993. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. 50: 1599–1609.

Pella, J.J. 1967. A study of methods to estimate the Schaefer model parameters with special reference to the yellowfin tuna fishery in the eastern tropical Pacific ocean. Ph.D. dissertation, University of Washington, Seattle, Wash. 156 p.

Pella, J.J., and P.K. Tomlinson. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 13: 419–496.

Polacheck, T., R. Hilborn, and A.E. Punt. 1993. Fitting surplus production models: comparing methods and measuring uncertainty. Can. J. Fish. Aquat. Sci. 50: 2597–2607.

Prager, M.H. 1994. A suite of extentions to a nonequilibrium surplus-production model. Fish. Bull. U.S. 92: 374–389.

Savoy, T.F., and V.A. Crecco. 1988. The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. Fish. Bull. U.S. 86: 467–481.

Schnute, J. 1985. A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42: 414–429.

Schnute, J. 1994. A general framework for developing sequential fisheries models. Can. J. Fish. Aquat. Sci. 51: 1676–1688.

Stocker, M., and C.M. Hand. 1993. Pacific cod. *In* B.M. Leaman and M. Stocker [ed.] Groundfish stock assessments for the west coast of Canada in 1992 and recommended yield options for 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1919: 407 p.

Talbot, G.B. 1954. Factors associated with fluctuations in abundance of Hudson River shad. Fish. Bull. U.S. 56: 373–413.

Walters, C. 1986. Adaptive management of renewable resources. McMillan Publishing Co., New York, N.Y.

Walters, C. 1990. A partial bias correction factor for stock–recruitment parameter estimation in the presence of autocorrelated environmental effects. Can. J. Fish. Aquat. Sci. 47: 516–519.

Walters, C. 1994. Lessons for stock assessment from the northern cod collapse. N. Am. J. Fish. Manage. In press.

Walters, C., and Collie, J.S. 1988. Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45: 1848–1854.

Walters, C.J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

Walters, C.J., and D. Ludwig. 1994. Calculation of Bayes posterior probability distributions for key population parameters: a simplified approach. Can. J. Fish. Aquat. Sci. 51: 713–722.

Walters, C., and A. Punt. 1994. Placing odds on sustainable catch using virtual population analysis and survey data. Can. J. Fish. Aquat. Sci. 51: 946–958.

Walters, C., M. Stocker, A.V. Tyler, and S.J. Westrheim. 1986. Interactions between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 43: 830–837.

Appendix: Numerical dynamic programming procedure

The solution of Eq. 9 for the function $B^*_{t+1}(B_t)$ is done on a discretized grid of B_t values. The simplest procedure is to set up a grid with $m + 1$ discrete, evenly spaced values of B for each t, with the ith value of B_t ($i = 0, 1, \ldots, m$) given by $B_{it} = B\min_t + i\Delta$, where $\Delta = (B\max_t - B\min_t)/m$. Start the procedure with $B\min_t = 0$ and $B\max_t = B_m$, where B_m, is a large enough biomass (or numbers) value to certainly be larger than the largest optimum estimate for any t. Define an array $S(i,t)$ to store the minimum sum of squares from time t forward to n for discrete state i, and an array $J(i,t)$ to store the index of the optimum conditional estimate B_{jt+1} for each state i at time t. Then perform the following steps.

(1) For each discrete state i at time n (terminal period), set $S(i,n) = (y(n) - qB(i,n))^2$.

(2) Working backward for $t = n - 1, n - 2, \ldots, 1$, do the following local minimization for each state i at time t: (2a) calculate $v = (y(t) - qB(i,t))^2$ (2b) for each possible next state j at time $t + 1$, calculate w_{t+1} using Eq. 3 with B_{it} and B_{jt+1} (do not include B_{jt-1} values less than g_tB_{it} as possible in this calculation). (2c) for each j, calculate $v^2 + Vw^2_{t+1} + S(j,t + 1)$ while saving j in $J(i,t)$ each time this sum is smaller than for a previous j tested (i.e., save the j that minimizes $v^2 + Vw^2 + S(j,t + 1)$).

(3) Find the initial state i at time 1 that minimizes $S(i,1)$, and record this B^*_{i1} as the optimum state estimate and the associated minimum sum of squares as S^*. Then loop over $t = 2, 3, \ldots, n$ and record the optimum state estimate B^*_{jt} as the one predicted from $J(i,t - 1)$ with i set to the optimum for time $t - 1$.

Refined estimates of the optimum state trajectory can then be obtained by successive approximation or "tunneling" along the solution path obtained in step 3. Set $B\min_t = B^*_{it} - 2\Delta$ and $B\max_t = B^*_{it} + 2\Delta$ for each t, reset Δ to $4\Delta/m$, and repeat steps 1–3 until Δ is tolerably small (actually, it is usually safe to set the state "band" checked to $B^*_{it} \pm \Delta$, rather than 2Δ, provided m is reasonably large, e.g., 20). In numerical experiments, I have found this tunneling procedure to be far faster than alternative procedures involving interpolation of optimum S and B estimates between the mesh points of a single, fixed grid.

While the procedure described above appears complex at first, it actually involves only a very short computer code (available from the author on request) and is extremely fast. For 20 years data with m = 10 and four tunneling improvement steps, a compiled QUICKBASIC version of the algorithm requires about 0.4 s to find the optimum B trajectory (and recruitment anomalies w) on an 80486 DX2/66 PC. This execution speed is important, since the algorithm would ordinarily be embedded within a procedure that tests or examines many alternative values for q, R, and possibly other uncertain parameters.

Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies

Kim N.I. Bell, Pierre Pepin, and Joseph A. Brown

Abstract: We report on an 18-month field study of temporal pattern and interrelationships of size- and age-at-recruitment (to fresh waters) for two diadromous hill-stream gobies in Dominica, West Indies (15°30′N, 61°25′W). Recruitment is panseasonal in *Sicydium punctatum* and *Sicydium antillarum* and supports a directed fishery similar to other goby fry fisheries. We found both size and age of recruits to vary seasonally, but the relationship of size to age is complex. Although positively related within lunar-monthly recruiting cohorts, the overall relationship of size and age was poor because seasonal variation in size is out of phase with age. Among recruiting cohorts, mean (or predicted) size and age are negatively correlated. Recruitment (fishery yield) also varies seasonally, in phase with size and out of phase with age. Peak fishery yields coincide with the youngest, but largest, recruits; low yields coincide with the reverse, implicating growth rate variations in fishery yield. This is the first such report of systematic seasonal variation in age-at-recruitment. Given these findings, size- and age-at-recruitment (here similar to settlement or metamorphosis) should not be assumed invariant, even for tropical fishes.

Résumé : Nous avons réalisé pendant 18 mois une étude sur le terrain du profil temporel et des relations entre la taille et l'âge au recrutement (dans les eaux douces) chez deux gobies diadromes des ruisseaux de montagne, en Dominique, aux Antilles (15°30′N, 61°25′W). Chez *Sicydium punctatum* et *Sicydium antillarum*, le recrutement est pansaisonnier et fait l'objet d'une pêche dirigée similaire à d'autres pêches de gobies pour les jeunes poissons. Nous avons observé que la taille et l'âge des recrues varient de façon saisonnière, mais que la relation entre la taille et l'âge est complexe. Bien que la relation taille–âge soit positive à l'intérieur de la cohorte de chaque mois lunaire, elle est peu marquée pour l'ensemble des cohortes, du fait que la variation saisonnière de la taille est déphasée par rapport à l'âge. Entre les cohortes de recrues, la taille et l'âge (moyens ou prédits) présentent une corrélation négative. Le recrutement (production de la pêche) varie aussi de façon saisonnière, en phase avec la taille et déphasé par rapport à l'âge. Les productions les plus élevées coïncident avec la présence des recrues les plus jeunes, mais les plus grandes; les faibles productions coïncident avec l'inverse, ce qui indique qu'il y a des variations de la production de la pêche liées au taux de croissance. C'est la première fois que l'on établit une telle variation saisonnière systématique de l'âge au recrutement. Étant donné nos résultats, il ne faut plus considérer comme invariables la taille et l'âge au recrutement (qu'on peut assimiler à l'installation sur le fond ou à la métamorphose), même chez les poissons tropicaux.

Introduction

Age-at-recruitment (here equivalent to planktonic larval duration, age-at-settlement, postlarval duration, etc.) in tropical fishes is often expressed for each location as a single value surrounded by some individual variation (e.g., Victor 1986; Radtke et al. 1988; Wellington and Victor 1989; Cowen 1991). Geographic variations have been the subject of increasing interest, but seasonal variations have not been found. Both Victor (1986) and Wellington and Victor (1989), while emphasising differences among species, report significant within-species geographic differences in planktonic larval duration, but they caution that temporal variations are not addressed by their data. Beckman et al. (1984) report differing growth rates of spot (*Leiostomus xanthurus*) between February–March and April–May. McCormick (1994) found short-term (days)

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variation in age of settling goatfish (*Upeneus tragula*) to be high but unstructured.

Variation of age within samples of recruiting, settling, or metamorphosing fish have been reported for several taxa (Victor 1986; Chambers and Leggett 1987; Radtke et al. 1988; Wellington and Victor 1989; Cowen 1991). The variation evident within a sample indicates a "window" of possible settlement ages, with a wider window permitting more sampling of settlement cues. Given that variation exists in single samples, it may exist over the temporal range of recruitment; this would be easiest to detect in panseasonally recruiting species.

Variation in age-at-recruitment is important because of its effect on cumulative survival. Cumulative survival (and therefore recruitment) is negatively related to time t, because it is the compounding factor for survival:

$$[1] \quad N_t = N_0 e^{-Zt},$$

where N is numbers at times 0 and t, and $-Z$ is the natural log of survival (Ricker 1975).

This paper represents the first step of probing for temporal patterns in age-at-recruitment, using *Sicydium* species.

Features of the life cycle of *Sicydium* species make them particularly suited to recruitment studies. Previous work (Bell 1994; Bell and Brown 1995) in Dominica, West Indies (15°30′N, 61°25′W) (Fig. 1) established the life cycle (Fig. 2). *Sicydium punctatum* is diadromous, with yolk-sac larvae hatching from nests in rivers and immediately becoming planktonic and drifting to the sea. The marine postlarval (after yolk absorption) period is followed by recruitment to fresh waters; during these return migrations, recruits are fished near river mouths. Following recruitment, adults remain in fresh water, spawning repeatedly. Adults are long lived (>5 yr) and iteroparous. Because spawning and recruitment occur panseasonally, all stages can be sampled year round. Parental stock, reproductive output, recruitment success, and growth rates can all be readily estimated. Times from egg to recruitment to the fishery (50–150 days) are short compared with temperate fishes, as are times from then to first reproduction (<12 months). An asset to both sampling and interpretation is that (e.g., Roughgarden et al. 1988) a biological transition coincides with recruitment to the artisanal fishery.

Such artisanal fisheries, for so-called goby fry (postlarvae ~12 to 25 mm SL) of sicydiine and other gobies are widespread and often substantial (Jordan and Evermann 1905; Montilla 1931; Koumans 1953; Manacop 1953; Ego 1956; Aboussouan 1969; Titcomb 1977). Fishery declines have been reported in the Philippines and the Caribbean (Manacop 1953; Blanco 1956; Ego 1956; Erdman 1961, 1986; Aiken 1988), but investigation of causes has been hampered by the lack of life-history information on these species.

Here, we investigate seasonal variation in age- and size-at-recruitment *S. punctatum* and *Sicydium antillarum* (both sensu Brockmann 1965), using data acquired over a 2-year period in Dominica (Fig. 1). *Sicydium antillarum* is morphologically quite similar to, but rarer than, *S. punctatum*. For comparison, we include some data on Dominican *Eleotris pisonis* (Gmelin), an eleotrid goby with a similar (Bell 1994) life history.

Methods

Source of samples

All fish samples were collected over a 19-month period, from October 1989 to April 1991 as newly recruiting fish, with some pigment and partial scalation. These features are good indicators of the stage of recruitment/settlement. Most samples were taken at a permanent upstream-migration trap at Canefield River (Fig. 1); a few samples were taken at other sites (Fig. 1) within a 15-km radius. This trap is a mesh cone whose large end faces downstream and leads upriver migrating fish (recruits) to a removable collection chamber, which is a modified funnel trap. The trap was designed to collect and maintain fish alive for several days and was checked daily during the recruitment part of the lunar month (4–10 days following the last lunar quarter) and less frequently at other times.

Samples were preserved in weak alcohol buffered with $NaHCO_3$ to saturation. Because laboratory grade ethanol was unobtainable on the island, we substituted white rum, approximately 40% ethanol. To compensate for its low ethanol content, the preservative in samples was replaced 1–2 days after initial preservation for most samples. Standard lengths reported are those taken on approximately 500 preserved specimens.

Identification

Adult *S. punctatum* and *S. antillarum* were identified according to Brockmann (1965) using morphology (dentition, lateral scale counts). Published keys at the species level do not cover prerecruit and early recruit stages, because pigment, dentition, and scalation all change during recruitment. Dentition, mouth, and body structure are sufficient to identify recruits as *Sicydium* spp. (Jordan and Evermann 1898) but not to the species level. To separate species, we identified recruiting postlarvae using pigment patterns that we had previously verified by rearing recruits until they acquired the adult characters (Bell 1994). These patterns (Fig. 3) are the most useful identifying features. Both species contain bars, those of *S. antillarum* are vertical, parallel pairs of brown bars on a lighter yellow-brown background, while *S. punctatum* has oppositely angled or crossed black bars in pairs (resembling the letters X, V, Y, I). Very early recruits completely lacking in pigmentation can be identified if kept for 1–3 days in freshwater aquaria to allow development of sufficient pigmentation to show patterns. A sample containing *S. punctatum* collected by us in Dominica is on deposit at the Smithsonian Institute, Washington, D.C. (catalogue No. USNM 314002). We caution that, following Hildebrand (1935), some workers (e.g., Aiken 1985; Erdman 1986; Penczak and Lasso 1991), synonymize (incorrectly, according to Brockmann 1965) several *Sicydium* spp. and call them *Sicydium plumieri*, sensu Erdman (1961). *Eleotris pisonis* were identified from adults following Jordan and Evermann (1898).

Amounts of postlarvae harvested during lunar-monthly recruitment episodes are those reported to us by fishers at Layou River, where return-migrant postlarvae are caught, and which we consider reliable. The fishery is a convenient indicator of recruitment intensity because it is

preferentially targeted toward tritri (goby postlarvae) when they are present. Unfortunately, there has never been a systematic collection of data for this or any similar fishery, the best (a 10-year series) information coming from Aboussouan (1969) in Réunion.

Otolith–age evaluation

Age was estimated for about 200 specimens, using dextral sagittal otoliths. Sagittae were the largest otoliths and had the clearest increments. We were not able to obtain or culture fish at marine stages preceding recruitment and were, therefore, not able to validate otolith increment periodicity for that stage. We assumed daily periodicity, since this is virtually the only periodicity that has been shown for larval fish under normal conditions (Jones 1992).

Otoliths (~500 μm in diameter) were extracted using glass microscalpels, then soaked in 60% H_2O_2 for at least several minutes to remove tissue residues, and then mounted with the convex side down in Crystalbond™ 509 clear thermoplastic adhesive (AREMCO Products Inc., Ossining, NY 10562-0429, USA.) on numbered glass slides. Grinding, polishing, or further cleaning were rarely needed.

Eroded otoliths were rejected if erosion had removed the entire outer edge, or used if the final increments could be counted. Erosion is readily detected because a jagged erosional profile replaces the smooth depositional profile of the otolith edge.

Ages (total) were obtained from counted sequences of individually measured increment widths. Increment widths were obtained under 50× (usually) or 100× (rarely) objectives of an Olympus BHC compound microscope (transillumination) fitted with a 10× intermediate lens and videocamera, and a frame-grabber board and video display. A rotatable polarizing filter on the light source often improved otolith readability. Sagittal otoliths (Fig. 4) of prerecruiting *S. punctatum* and *S. antillarum* postlarvae are nonsymmetrical as viewed, like the shape of a wide hand print, and the growth emphasis is in the direction of the fingers. The transect used for increment measurement and counting was chosen to cross increments at their greatest widths (near the 12 o'clock position in Fig. 4).

Increment counts were done blind (with reference only to the otolith reference number), beginning at the center of the crystal (primordium; rodlike feature) at the origin, taking the distances to the end of the crystal, to precore increments if visible, to the core (circular feature), and to subsequent increments (not circular) until recruitment. Because the center of the otolith is the most difficult to read, we assumed that all possessed the features seen in those that were clear in that region: there is usually only one increment within the core, so the core is the third feature digitized. Because hatching is usually 24–48 h (Bell 1994) after fertilization, the core is probably a hatch check, but we have not yet confirmed this and have not adjusted ages to reflect this. No otoliths requiring adjustment after the core feature were used in these analyses, but similar analyses (Bell 1994), which included adjusted otoliths, gave virtually identical results. Increments visible only in a transect outside the growth-emphasis sector near the 12 o'clock position were counted and digitized on the 12 o'clock transect with a coding to indicate that those widths were not usable, but that the cumulative width indicated to the next on-transect visible increment remained accurate. Subsequent increments up to the edge of the otolith were then taken. Repeated blind readings (in the same or later sessions) showed good matches of increment width sequences, and were usually exact or within 1, rarely ≥3, increment.

Fig. 1. Collection sites for recruiting gobies (●) and towns (○) in Dominica, West Indies.

Various workers (e.g., Victor 1986; Wellington and Victor 1989; Campana 1992) have discussed "subdaily" increments, but not all agree that these are real. We counted only those features we could confidently describe as increments, avoiding those which could be explained as optical artefacts. Features that could be focused to near-invisibility while keeping both adjacent increments in focus were not counted as increments.

The recruitment feature was by definition the outer edge of the otolith (as in Fig. 4) where the fish was captured at entry to fresh water. In cultured fish, or fish captured postrecruitment, it was identified by an altered growth direction in the otolith. This feature is comparable with reported settlement marks (e.g., Wellington and Victor 1989), but clearer than that reported by Victor (1982) for *Thalassoma bivittatum*. The stage in recruitment was also evident from the external pigmentation, mouth structure, behaviour of fish and their location: early recruits (no pigment, terminal mouth) and late recruits (pigmented, subterminal mouth) are separated by only 1–5 days yet are very easily distinguished.

The analyses of age use information from 143 newly recruited fish: 117 *S. punctatum*, and 25 *S. antillarum*

Fig. 2. Life cycle (above appropriate habitat) of sicydiine gobies in Dominica (Pyriform stalked eggs under stones, vertically swimming and drifting larva absorbing yolk over 5–8 d, recruiting at 50–150 d to fresh waters and to fishery.)

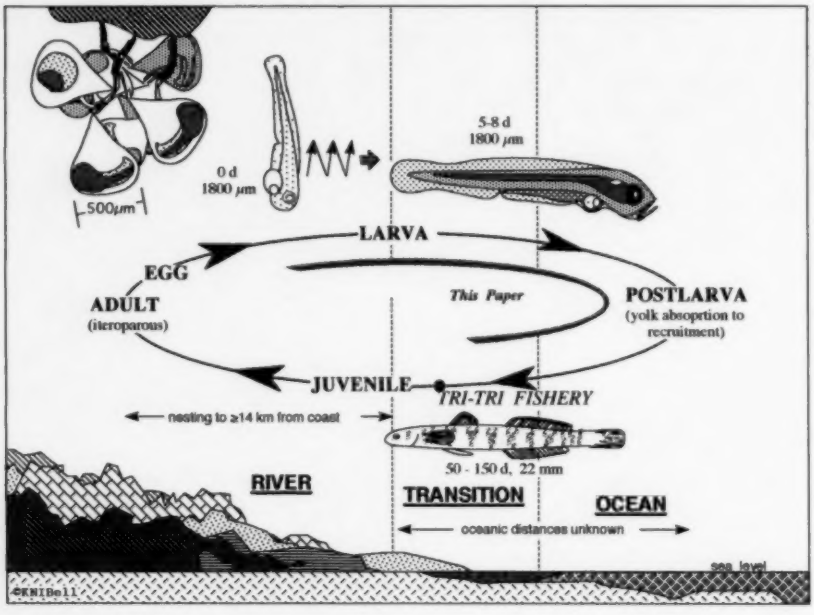
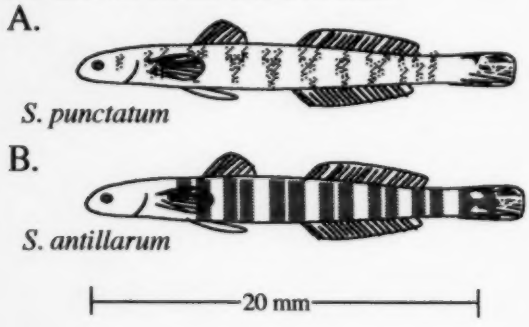


Fig. 3. Diagnostic features of recruiting *Sicydium punctatum* and *S. antillarum* (sensu Brockmann 1965) in Dominica, W.I. See Introduction for details.



otoliths that could be read from the core to the recruitment feature (or edge) and did not require adjustment.

Analysis of seasonal variations

Recruitment is panseasonal and periodic for *Sicydium* species in Dominica, and elsewhere in the Caribbean (Erdman 1986), as for *Sicyopterus extraneus* in the Philippines (Manacop 1953). As indicated by the commercial fishery and catches in our upstream-migration traps (Bell 1994), recruitment episodes tend to begin on the fourth day following the last lunar quarter (Fig. 5) and continue with diminishing intensity for several days. Such lunar-phased recruitment episodes are a useful way of defining recruiting cohorts. We consider each episode to begin on the day of the last lunar quarter (LLQ) and end on the day preceding the next. Thus, "LLQ *n*" (in text or figures) denotes the *n*th sequential last-lunar-quarter recruitment episode observed during this study, with LLQ 1 beginning May 27, 1989; LLQ 2 beginning June 26, 1989; and so on.

To evaluate whether periodic functions of time could explain variations in the dependent variables length-at-recruitment, age-at-recruitment, and numbers recruiting, we applied techniques similar to those of Batschelet (1981) and Zar (1984). ANOVA is a legitimate technique with periodic (or circular) data, provided residuals are independently and normally distributed, and least squares provides an unbiased fit even if these assumptions are not met (Batschelet 1981, p. 160). Sinusoidal variation (with a frequency of 1) in a Y variable over a cycle can be expressed as

$$[2] \quad Y = b + m(\cos(RX + \partial)),$$

where RX is the angular transformed independent X variable (day of year (DOY), time of day, etc.), and b is an intercept, m is the slope, and ∂ is the phase lag.

While Eq. 2 can be fitted iteratively by varying ∂, it is equivalent (Batschelet 1981) to

$$[3] \quad Y = \beta_0 + \beta_1\sin(RX) + \beta_2\cos(RX)$$

where β_1 and β_2 are coefficients, and β_0 is a mean level, equivalent to an intercept in a nonperiodic regression. (Here we use the azimuthal system, in which an angle α is measured in a clockwise direction from the positive Y axis,

as on a compass.) Equation 3 can be solved directly using $\sin(RX)$ and $\cos(RX)$ as new variables. Batschelet (1981, p. 164) states "... to obtain meaningful results ... a minimum of $n = 6$ equally spaced [data points] will suffice... however, if the intervals are not equal, at least $n = 8$ data points are required." He also points out that reliability of estimation of the parameters will suffer if all the points are clustered in a single narrow section or phase of the cycle.

Location of peaks (P) can be determined by visual inspection of plots, or by algebra provided by Batschelet (1981, sec. 8.2). Where the position of the peak (P_p) is ∂ units (here in degrees) after the nominal zero of the cycle (t_0),

$$[4] \quad P_p = t_0 + \partial$$

$$[5] \quad \partial' = \arctan(\beta_1/\beta_2)$$

$$[6] \quad \partial = \partial' + QC$$

where QC is a quadrant correction to be added to ∂': QC = 0° if (β_1,β_2) are (+,+); QC = 180° if (+,−) or (−,−), and QC = 360° if (−,+).

Dates (independent variables) were first transformed into circular variables (RDOY) by multiplying DOY (0–365) by $2\pi/365$ to obtain an equivalent radian measure, or by 360/365 for degrees. For solution as (3) the proxy X-variables become sin(RDOY) and cos(RDOY).

Residuals were examined for trends with respect to the untransformed time variable (DOY). The curves represented by the regressions were then expressed on DOY axes by tracing fitted values.

Growth indices

A linear length-based average growth index (G_L, millimetres per day) was calculated as

$$[7] \quad G_L = (SL - 1.8)/age_{hatch}$$

where SL is the standard length in millimetres, 1.8 is the size in millimetres of a newly hatched larva (Bell 1994), and age_{hatch} is total age (days) less three.

Results

The mean age at recruitment of *S. punctatum* was 83.4 ± 1.3 (mean ± SE) days (range 54–136, $n = 117$), and for *S. antillarum* was 86.7 ± 3.4 d (range 63–139, $n = 25$). The mean SL for *S. punctatum* was 19.5 ± 0.1 mm (range 16–25, $n = 324$), and for *S. antillarum* was 21.8 ± 0.8 mm (range 18.8–25.5, $n = 78$). Although the overall (all seasons pooled) correlations of age and size for *S. punctatum* and *S. antillarum* are not significant (Fig. 6*b*), within most lunar-monthly recruitment episodes (LLQs) the relationships are all positive and often significant (Fig. 6*c*, Table 1). All correlations thus obtained ($0.25 \leq r^2_{LLQ} \leq 0.89$; Table 1) far exceed those obtained by pooling all samples ($r^2 \leq 0.02$), clearly indicating temporal variation in this relationship. For *S. punctatum* there are 11 LLQs with >2 points; of these, six are significant ($0.0001 \leq p \leq 0.05$) and two are marginally so ($0.05 \leq p \leq 0.1$). For *S. antillarum* there are four LLQs with >2 points; of these, one is highly significant, one is marginal, and two are not significant.

Contrasting with the positive relationship of (individual) size and age found within LLQs, the relation of (mean) size and age is negative across LLQs (Fig. 7). Samples from similar months of different years are also similar on this plot. The negative trend is significant ($p < 0.05$) for *S. punctatum* but marginal ($0.05 < p < 0.1$) for *S. antillarum*, which shows a similar trend but for which there are fewer observations.

Age-at-recruitment varies seasonally (Fig. 8*a*, Tables 1 and 2) and is nearly 180° out of phase with, or is inverse

Fig. 4. Sagittal otolith of newly recruited *Sicydium punctatum*. Nucleus is visible below centre.

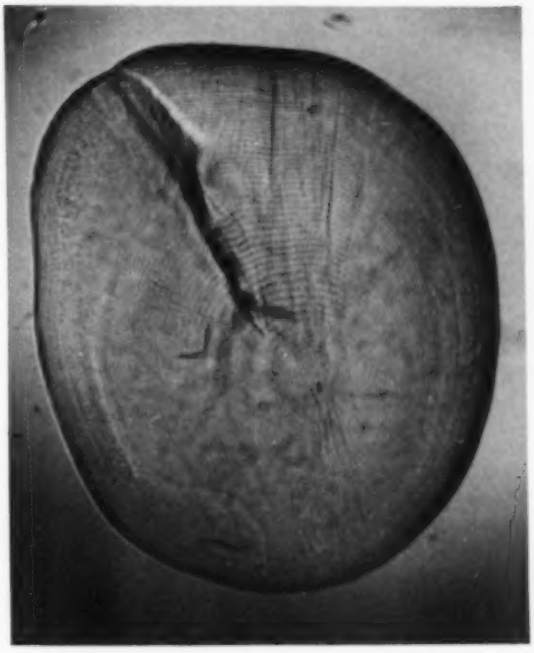


Fig. 5. Lunar-monthly recruitment pattern (numbers caught in upstream-migration trap). Because zeros cannot occur on a logarithmic axis, an artificial zero is marked "0" to show zero catches.

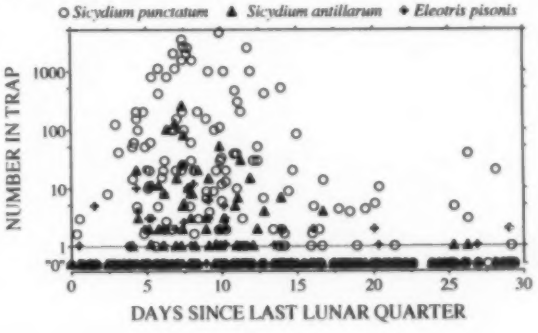
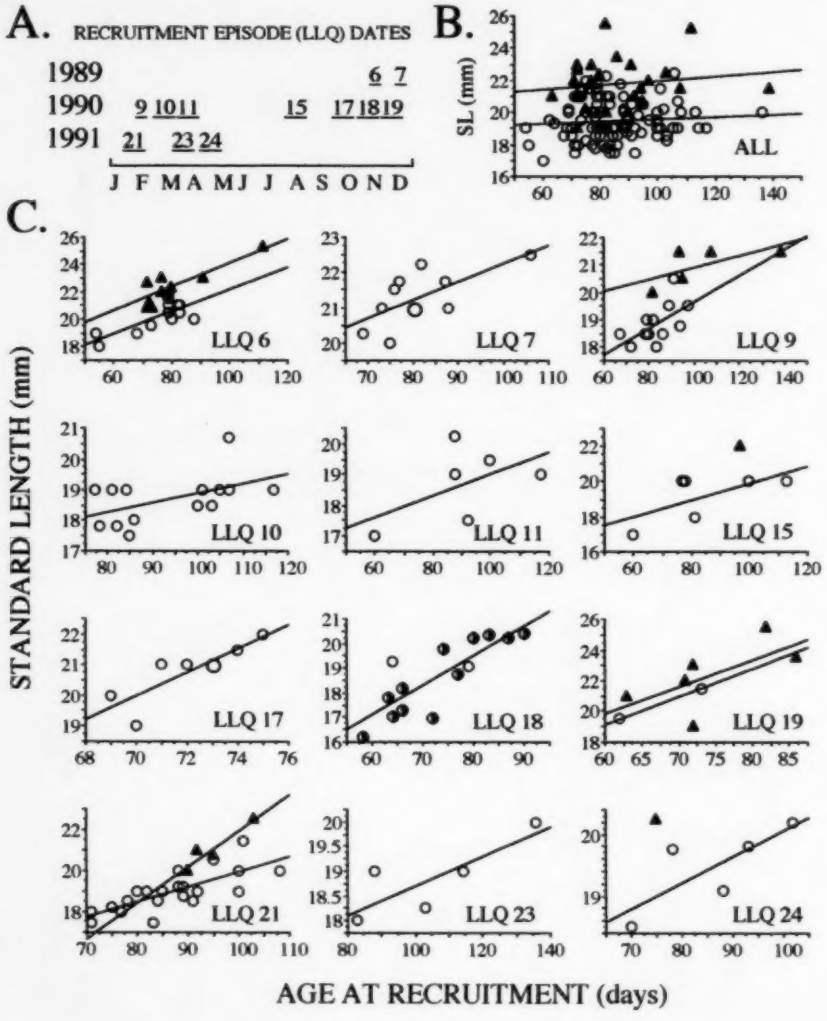


Fig. 6. Temporal variation of age-at-recruitment in relation to standard length. "LLQ" refers to sequential number of last-lunar-quarter recruitment episode. (A) Dates of last lunar quarters. (B) Overall length–age relationship. (C) Length–age relationship within each recruitment episode (regressions summarised in Table 1). (○) *S. punctatum*; (▲) *S. antillarum*. With the exception of LLQ 18, in which 12 *S. punctatum* were cultured ~29 d (◑) following recruitment, all length measurements are taken on fish cultured ≤4 d after capture. Coincident points are indicated by larger symbols. See also Table 1.



to, the seasonal variation in length-at-recruitment (Fig. 8*b*, Table 2). Both variations are significant ($p < 0.05$), for either species or in combination, and species are in phase with each other.

Where seasonal variation in size- and age-at-recruitment is not concordant, growth rate cannot be inferred from age-at-recruitment alone. For these data, variation in age-at-recruitment underestimates variation in growth rate because age and size variations are nearly 180° out of phase. The linear growth rate index (G_L; Eq. 7) is strongly seasonal for both *S. punctatum* and *S. antillarum*, peaking at recruitment dates in September–October, and lowest for March–April recruits (Fig. 8*c*).

The directed fishery (Fig. 8*d*) for return-migrant postlarvae at Layou River has its highest yields in the fall. However, even in that season there is much short-term variability such that yields can be either large or nonexistent. Yields in the spring are reported to typically vary from nil to one barrel (80 L), which is consistent with our data. Thus, both magnitude and month-to-month variability

Table 1. Regressions of length against age-at-recruitment by species and recruitment episode (LLQ) as $SL = \beta_0 + \beta_1 AGE$. See also Fig. 6.

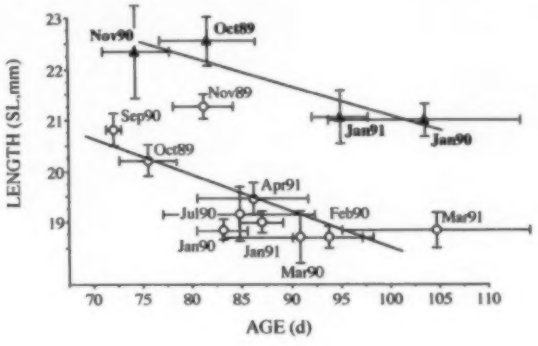
	N	r^2	p	β_0	β_1
All LLQs					
S. punctatum	105	0.006	0.4306	25.35	0.008
S. antillarum	25	0.006	0.7111	25.258	0.008
LLQ 6					
S. punctatum	13	0.576	0.0026	14.191	0.08
S. antillarum	8	0.789	0.0032	15.511	0.086
LLQ 7					
S. punctatum	11	0.461	0.0217	17.025	0.052
LLQ 9					
S. punctatum	12	0.355	0.0409	14.856	0.048
S. antillarum	5	0.441	0.2214	18.771	0.022
LLQ 10					
S. punctatum	14	0.254	0.0661	15.84	0.03
LLQ 11					
S. punctatum	6	0.283	0.277	15.52	0.035
LLQ 15					
S. punctatum	6	0.434	0.1551	15.213	0.047
LLQ 17					
S. punctatum	8	0.726	0.0072	−7.132	0.387
LLQ 18					
S. punctatum	14	0.674	0.0003	9.911	0.12
LLQ 19					
S. antillarum	6	0.424	0.161	9.347	0.175
LLQ 21					
S. punctatum	21	0.578	0.0001	12.518	0.075
S. antillarum	4	0.894	0.0542	4.583	0.173
LLQ 23					
S. punctatum	5	0.663	0.0934	15.718	0.03
LLQ 24					
S. punctatum	5	0.623	0.1126	15.833	0.042

Note: Regressions included only otoliths from fish cultured ≤4 days following capture, except in LLQ 18 (12 specimens cultured ≤29 days, identified by symbols in Fig. 7).

appear to vary seasonally. Much of the variation in fishery yield (in barrels, BBL) is accounted for by a periodic regression (Table 2). The calculated peak yield (Eqs. 4–6) is on DOY = 296, or October 23. Despite the acceptable correlation however, the cosine curve (Fig. 8*d*) appears excessively symmetrical for the fishery profile, which has a narrow peak of high yields and a wide trough with low yields. Highs and lows in the landings coincide with extremes in the age- and size-at-recruitment curves, and are in phase with the size and growth curves and ~180° out of phase with the age curve.

Relationships of age-at-recruitment and growth with hatch (Fig. 9) date are less strong (Table 2) than relationships with recruitment date (Fig. 8), for both *Sicydium* species (10–20% less variation explained by hatch date). Age-at-recruitment is at a minimum for larvae hatching in the summer (June–August) and a maximum for larvae hatching in the winter (December–January). Growth (G_L) expected as a function of hatch date is about 0.21 mm·d^{-1} in the winter, and rising by about 30% to peak (0.29 mm·d^{-1}) in the summer. The middle to late summer, thus, appears to be the optimal hatch period for rapid growth.

Fig. 7. Correlation of mean length (SL) and mean age of *S. punctatum* and *S. antillarum* among LLQs. The relationship is opposite to that within LLQs. Mean values for each LLQ (±1SE) are plotted. (○) *S. punctatum*; (▲) *S. antillarum*. Regression for *S. punctatum* is SL = 25.597 − 0.071(age), $r^2 = 0.495$, $n = 10$, $p = 0.0232$; *S. antillarum*: SL = 26.782 − 0.057(age), $r^2 = 0.838$, $n = 4$, $p = 0.08$. Month of recruitment for each sample is indicated in plain and bold type for *S. punctatum* and *S. antillarum* respectively.

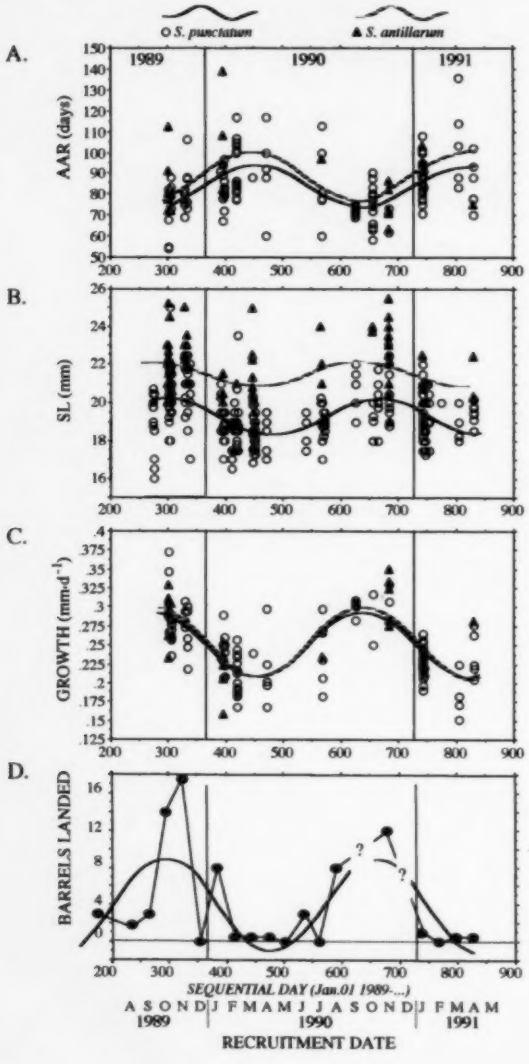


Discussion

Seasonal variation is evident (Fig. 8) in age and length at recruitment for *S. punctatum* and *S. antillarum*, and in fishery landings (an indicator of recruiting numbers) for a mixture of species in which *S. punctatum* predominates (~95%). The variations repeat in data covering nearly 2 years, supporting interpretation as recurring annual cycles. The seasonal variations in age, size, and growth have virtually identical phases with respect to time of year in *S. punctatum* and *S. antillarum*. The opposite phasing of the size- and age-at-recruitment curves restates what is shown in Fig. 7: among cohorts, the predicted age-at-recruitment is negatively related to predicted SL, and contrasts with the positive individual age–size relationship within cohorts.

The phase of the seasonal variation differs among variables. Maximum recruitment is associated with cohorts having the greatest mean size *and* the lowest mean ages. Recruitment (with migration to fresh waters) is therefore not determined by either size or age alone, but by both in combination: the "decision line" for each species is approximated by the regressions in Fig. 7; individual growth trajectories would cross them near recruitment. The regressions should perhaps be curvilinear, but the point is moot with these data. The contrary variation of size versus age within and among LLQs (recruiting cohorts) is a strong caution against the application of a single age–length key across seasons. It is also a generally useful pointer to temporal variation in growth rates.

Fig. 8. Seasonal cyclic trends in Dominica 1989–1991 with respect to date of recruitment, indicated by calendar month and sequential day number from Jan. 1, 1989. (○) *S. punctatum*; (▲) *S. antillarum*. (A) Age-at-recruitment (AAR). (B) Length (millimetres). (C) Growth index (millimetres per day). (D) Fishery landings (barrels) at Layou River, Dominica (missing data indicated by question marks). Regression equations are given in Table 2.



The maximum growth rate occurs in larvae hatched near midsummer, while the maximum recruitment (fishery landings) occurs in the fall. Similarly, the minimum growth rate occurs in larvae hatched in late December, while minimum recruitment occurs in April. A peak or trough in recruitment follows a peak or trough in growth rate with a lag that approximates age-at-recruitment. A positive association of growth rate and fishery yield is consistent with theory (Houde 1987). More directly, the age-at-recruitment estimates give the time over which prerecruitment mortality operates. While much effort has in the past been directed at variations in daily mortality rates, we suggest that the increasing availability of precise age data from otoliths justifies an increased emphasis on the role of temporal variation in age-at-recruitment and growth rates in recruitment variation.

We know of no previous similar report of systematic cyclic seasonal variation in age at recruitment. This variation is qualitatively different from that reported within single samples (e.g., Victor 1982, 1986; Radtke et al. 1988; Wellington and Victor 1989; Cowen 1991; McBride and Conover 1991; McCormick 1994). Even at a single location, age- and size-at-recruitment are clearly not always constant, but can be functions of time. These seasonalities point to causes other than variation in reproductive output as candidate sources of variation in fishery yields. When relationships between spawning and recruitment are sought (e.g., Robertson 1990), the possible existence of seasonal variation in the period from spawning to recruitment should be taken into account, or the assumption of invariant age-at-recruitment should be acknowledged as a source of uncertainty.

Comparison with other gobiids

Dominican diadromous gobies (three species: *S. punctatum*, *S. antillarum*, *E. pisonis*) have shorter planktonic durations (Fig. 10) than do the two Hawaiian species reported on by Radtke et al. (1988): 85.9 versus 144 d overall ($F_{1,234} = 293.0$, $p < 0.001$). In Dominica the recruitment of *Sicydium* spp. occurs sooner ($F_{1,212} = 362.5$, $p < 0.001$) than it does for Hawaiian *Awaous stamineus* and *Stenogobius genivittatus*, yet despite quicker recruitment both *Sicydium* species recruit at a larger size, indicating more rapid growth. *Eleotris pisonis*, with the highest mean age-at-recruitment in Dominica seen so far, also has lower age-at-recruitment ($F_{1,43} = 71.7$, $p < 0.001$) than the Hawaiian species, and although smaller than *Sicydium* recruits it is older at recruitment. The data for *S. punctatum* and *S. antillarum* show more scatter than the Hawaiian species, because the Dominican data cover a greater temporal range (all seasons, 2 years) than the Hawaiian data (a single sample from Oahu, early June 1986). Given that species-based variation exists in growth rates in Dominica, the difference between Dominican and Hawaiian data is plausibly the sum of differences due to both species and habitat. This difference between Hawaii and the Caribbean parallels that found in other families as well: we used one-way ANOVA to compare within-family planktonic larval durations in the Caribbean and Hawaii, using the species means for Labrids and Pomacentrids from Victor (1986) and Wellington and Victor (1989). (Because use of species means entails a loss of degrees of freedom, this method should be conservative.) Labrids have significantly longer planktonic durations in Hawaii (55 days vs. 40 days, $F_{1,37} = 4.95$, $p < 0.05$), while Pomacentrids have nonsignificantly longer planktonic durations in Hawaii (26 days vs. 23 days, $F_{1,21} = 2.99$, $p > 0.05$). Thus, all three groups show a difference, significant in two groups, in the same direction

Table 2. Relation of age-at-recruitment, length-at-recruitment, average growth-to-recruitment, and fishery landings to recruitment date, and of age and growth to hatch date, for *S. punctatum* and *S. antillarum*. See also Figs. 8 and 9.

Parameter	Equation	Peak	r^2	n	p
Relationships with recruitment date					
Age-at-recruitment[a] (days)					
Age	= Int + $\beta_1$sin(RDOY) + $\beta_2$cos(RDOY)				
S. punctatum	= 83.835 + 10.1sin(RDOY) − 0.213cos(RDOY)		0.28	117	0.0001
	p = 0.0001 p = 0.9243	April 02			
S. antillarum	= 89.077 + 12.42sin(RDOY) − 2.12cos(RDOY)		0.238	25	0.0503
	p = 0.0203 p = 0.7878	April 11			
Length-at-recruitment[b] (SL, mm)					
SL	= Int + $\beta_1$sin(RDOY) + $\beta_2$cos(RDOY)				
S. punctatum	= 19.3 − 0.87sin(RDOY) + 0.411cos(RDOY)		0.249	324	0.0001
	p = 0.0001 p = 0.0004	October 26			
S. antillarum	= 21.62 − 0.6sin(RDOY) − 0.017cos(RDOY)		0.079	78	0.0462
	p = 0.0148 p = 0.9665	September 28			
Growth[b] (mm·d^{-1})					
Growth	= Int + $\beta_1$sin(RDOY) + $\beta_2$cos(RDOY)				
S. punctatum	= 0.25 − 0.042sin(RDOY) − 0.002cos(RDOY)		0.496	105	0.0001
	p = 0.0001 p = 0.7196	September 27			
S. antillarum	= 0.26 − 0.051sin(RDOY) − 0.004cos(RDOY)		0.469	25	0.0009
	p = 0.0003 p = 0.8466	September 26			
Fishery yield (at Layou, barrels, all species, ~99% *Sicydium*)					
Barrels	= Int + $\beta_1$sin(RDOY) + $\beta_2$cos(RDOY)				
Barrels	= 4.112 − 4.807sin(RDOY) + 1.979cos(RDOY)		0.46	19	0.007
	p = 0.003 p = 0.163	October 23			
Relationships with hatch date					
Age-at-recruitment[a]					
Age (d)	= Int + $\beta_1$sin(RHDOY) + $\beta_2$cos(RHDOY)				
S. punctatum	= 79.513 − 0.794sin(RHDOY) + 8.593cos(RHDOY)		0.179	117	0.0001
	p = 0.7462 p = 0.0001	December 25			
S. antillarum	= 85.636 + 1.038sin(RHDOY) + 5.486cos(RHDOY)		0.031	25	0.7056
	p = 0.8917 p = 0.4159	January 10			
Growth[b]					
Growth	= Int + $\beta_1$sin(RHDOY) + $\beta_2$cos(RHDOY)				
S. punctatum	= 0.252 + 0.001sin(RHDOY) − 0.039cos(RHDOY)		0.375	105	0.0001
	p = 0.94 p = 0.0001	May 30			
S. antillarum	= 0.257 − 0.005sin(RHDOY) − 0.04cos(RHDOY)		0.201	25	0.0845
	p = 0.8 p = 0.0288	June 08			

Note: RDOY = DOY(2π/365) (i.e., DOY transformed to radians of year), RHDOY is same but for hatch date (= DOY_{rec} − Age + 3). Regressions are of the form $Y = C + \beta_1\sin(RDOY) + \beta_2\cos(RDOY)$ (see Methods), with parameter significance and calculated peak date on following line. For growth calculation and relationships with hatch date, age is adjusted by −3 to exclude features within the core, assumed to be deposited at hatch when the length is ~1.8 mm.

[a]Using fish cultured 0–30 d.

[b]Using fish cultured 0–4 d.

(age-at-recruitment in Hawaii is greater than in Dominica). If more data are acquired on other species in Dominica and Hawaii to obtain a better control of species-related differences, insights into habitat differences may follow.

Implications

Over longer terms (than seasons), such as years in temperate and northern fisheries, variations in growth rate are acknowledged by the frequent reevaluation of age–length relationships. However, this has been directed at estimating numbers in each year-class. Terms of the equation $N_t = N_0e^{-Zt}$ include most acknowledged contributors to cohort strength. We feel the effect of t on gross survival has been unduly subordinated to questions centering on the role of mortality rates or larval production. We observe that, whether mortality is higher or lower for younger or older, larger or smaller, fast-growing or slow-growing larvae, the compounding effect of t (age-at-recruitment) on cumulative mortality can readily supersede the effect of all but the most extreme short-term variations in daily mortality.

An initial motivation for this study was an elucidation of factors which could contribute to fishery variations,

Fig. 9. Seasonal cycles with respect to hatch date, for *S. punctatum* (○) or *S. antillarum* (▲). Hatch dates are indicated as day numbers beginning with January 1, 1989; letters below *x*-axis indicate months. (A) Days hatch-to-recruitment (= AAR − 3). (The angled alignment of age-at-recruitment points in each sample has no meaning here; it merely results from the fact that, for each point *i*, $X_i + Y_i$ = collection date). (B) Growth index (millimetres per day) against hatch date. Regression equations are given in Table 2.

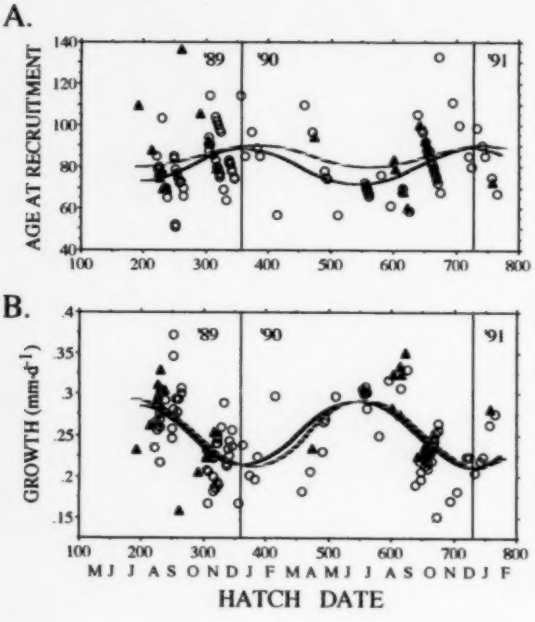
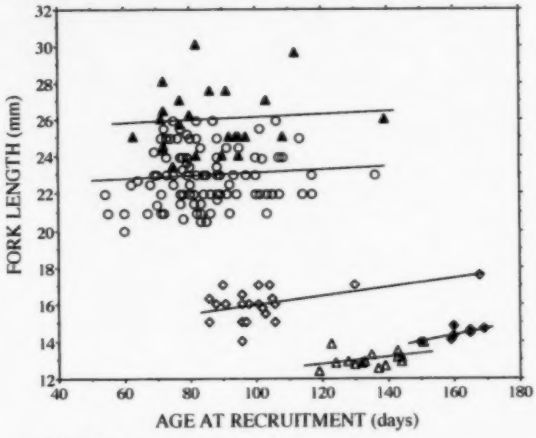


Fig 10. Comparison of recruit length-at-age for diadromous gobies in Dominica (three species) and from Hawaii (two species; Radtke et al. 1988), with regression lines. (Fork lengths are used to enable comparison with published data.) Hawaiian data are from single collections, *Eleotris pisonis* are mostly from a single collection, while *Sicydium* data are from multiple seasons.



DOMINICA (upper 3 clusters)
○ *Sicydium punctatum* $y = 0.008x + 25.35$; $n = 105$, $r^2 = 0.006$, $p = 0.43$
▲ *Sicydium antillarum* $y = 0.008x + 25.258$; $n = 25$, $r^2 = 0.006$, $p = 0.71$
◇ *Eleotris pisonis* $y = 0.023x + 13.6$; $n = 21$, $r^2 = 0.23$, $p = 0.028$
HAWAII (lower 2 clusters, data from Radkte & Kinzie, 1988)
△ *Stenogobius genivittatus* $y = 0.019x + 10.5$; $n = 15$, $r^2 = 0.15$, $p = 0.15$
◆ *Awaous stamineus* $y = 0.038x + 8.25$; $n = 8$, $r^2 = 0.508$, $p = 0.047$

especially the apparent declines (Manacop 1953; Blanco 1956; Ego 1956; Erdman 1961; Erdman 1986; Aiken 1988) reported in goby fry fisheries. The results discussed here identify variations in age-at-recruitment (associated with variation in growth rate) as potential contributors to fishery variation among seasons. Such variation may exist as well over longer (e.g., annual, decadal, etc.) timescales responding to, for example, environmental and climatic changes. Spatial variations as shown by Victor (1986) and Wellington and Victor (1989) for damselfishes and wrasses appear to apply also for gobiids in general.

We have demonstrated significant variation over seasons in recruit age, growth history and size; these are relevant to the recruitment of these tropical species. Furthermore, these species may represent over short periods and in a more structured way (seasons) what happens in temperate situations over years instead of months; if so, these species may be ideal systems in which to study recruitment processes. We believe age and growth are the major factors determining recruitment in *Sicydium* species in Dominica, but we caution that variations in reproduction could occur and also contribute to recruitment variation (Bell 1994). Because of the complexity of modelling recruitment with variable time lags, we defer further exploration of this question to subsequent papers.

Acknowledgments

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References

Aboussouan, A. 1969. Note sur les «Bichiques» de l'île de la Réunion. Recl. Trav. Stn. Mar. Endoume Mars. Fasc. Hors Sér. suppl. 1969(9): 25–31.

Aiken, K.A. 1985. *Sicydium plumieri* (Bloch) a migratory fish from Jamaica rivers. Nat. Hist. Notes Nat. Hist. Soc. Jamaica, 1(10): 35–39.

Aiken, K.A. 1988. Notes on the ecology of fishes of some rivers in Portland. Nat. Hist. Notes Nat. Hist. Soc. Jamaica, 2(2): 9–19.

Batschelet, E. 1981. Circular statistics in biology. Mathematics in biology series. *In* R. Sibson and J. Cohen [ed.] Academic Press, London. 371 p.

Beckman, D.W., J.M. Dean, and B.W. Baruch. 1984. The age and growth of young-of-the-year spot, *Leiostomus xanthurus* Lacépède, in South Carolina. Estuaries, 7: 487–496.

Bell, K.N.I. 1994. Life cycle, early life history, fisheries and recruitment dynamics of diadromous gobies of Dominica, W.I., emphasising *Sicydium punctatum* Perugia. Ph.D. thesis, Memorial University, St. John's, Nfld. 275 p.

Bell, K.N.I., and J.A. Brown. 1995. Active salinity choice and enhanced swimming endurance in 0 to 8-d-old larvae of diadromous gobies, including *Sicydium punctatum* (Pisces), in Dominica, W.I. Mar. Biol. 121: 409–417.

Blanco, G.J. 1956. Assay of the goby fry (ipon) fisheries of the Laoag River and its adjacent marine shores, Ilocos Norte Province. Philipp. J. Fish. 4: 31–80.

Brockmann, F.W. 1965. A taxonomic study of the Panamanian freshwater gobies of the genera *Awaous* and *Sicydium*. M.S. thesis, Florida State University, Tallahassee, Fla. 73 p.

Campana, S.E. 1992. Measurement and interpretation of microstructure of fish otoliths, p. 59–71. *In* D.K. Stevenson and S.E. Campana [ed.] Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. 117.

Chambers, R.C., and W.C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Can. J. Fish. Aquat. Sci. 44: 1936–1947.

Cowen, R.K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. Mar. Ecol. Prog. Ser. 69: 9–15.

Ego, K. 1956. Life history of freshwater gobies. Project 4-4-R. Freshwater and Game Fish Management Resources, Department of Lands and Natural Resources, Honolulu, Hawaii. 23 p.

Erdman, D.S. 1961. Notes on the biology of the Gobiid fish *Sicydium plumieri* in Puerto Rico. Bull. Mar. Sci. Gulf Caribb. 11: 448–456.

Erdman, D.S. 1986. The green stream goby, *Sicydium plumieri*, in Puerto Rico. Trop. Fish Hobbyist, 1986 (February): 70–74.

Hildebrand, S.F. 1935. An annotated list of the fishes of the freshwaters of Puerto Rico. Copeia, 1935: 49–56.

Houde, E.D. 1987. Fish Early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29.

Jones, C.M. 1992. Development and application of the otolith increment technique, p. 1–11. *In* D.K. Stevenson and S.E. Campana [ed.] Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. 117.

Jordan, D.S., and B.W. Evermann. 1898. The Fishes of North and Middle America. Bull. U.S. Natl. Mus. 47. Part 3. U.S. National Museum, Washington.

Jordan, D.S., and B.W. Evermann. 1905. The aquatic resources of the Hawaiian Islands. Bull. U.S. Fish Comm. 1903. Part I. The shore fishes. Vol. 23. U.S. Fish Commission, Washington, D.C.

Koumans, F.P. 1953. Gobioidea. Vol. X. The fishes of the Indo-Australian Archipelago series. *In* M. Weber and L.F. de Beaufort [ed.] E.J. Brill, Leiden, Germany. 423 p.

Manacop, P.R. 1953. The life history and habits of the goby, *Sicyopterus extraneus* Herre (añga) Gobiidae with an account of the goby-fry fishery of Cagayan River, Oriental Misamis [Province, Mindanao, Philippines]. Philipp. J. Fish. 2: 1–60.

McBride, R.S., and D.O. Conover. 1991. Recruitment of young-of-the-year bluefish *Pomatomus saltatrix* to the New York Bight: variation in abundance and growth of spring- and summer-spawned cohorts. Mar. Ecol. Prog. Ser. 78: 205–216.

McCormick, M.I. 1994. Variability in age and size at settlement of the tropical goat fish *Upeneus tragula* (Mullidae) in the northern Great Barrier Reef lagoon. Mar. Ecol. Prog. Ser. 103: 1–15.

Montilla, J. 1931. The ipon fisheries of northern Luzon. Philipp. J. Sci. 45: 61–75.

Penczak, T., and C. Lasso. 1991. Problems of estimating population parameters and productions of fish in a tropical rain forest stream, North Venezuela. Hydrobiologia, 215: 121–133.

Radtke, R.L., R.A. Kinzie, and S.D. Folsom. 1988. Age at recruitment of Hawaiian freshwater gobies. Environ. Biol. Fishes. 23: 205–213.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Robertson, D.R. 1990. Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. J. Exp. Mar. Biol. Ecol. 144: 49–62.

Roughgarden, J., S. Gains, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. Science (Washington, D.C.), 241: 1460–1466.

Titcomb, M. 1977. Native use of fish in Hawaii. 2nd ed. University Press of Hawaii, Honolulu, Hawaii. 180 p.

Victor, B.C. 1982. Daily otolith increments and recruitment in two coral reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. 71: 203–208.

Victor, B.C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). Mar. Biol. 90: 317–326.

Wellington, G.M., and B.C. Victor. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Mar. Biol. 101: 557–567.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J. 718 p.

Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario[1]

Peter S. Rand, Donald J. Stewart, Brian F. Lantry, Lars G. Rudstam, Ora E. Johannsson, Andrew P. Goyke, Stephen B. Brandt, Robert O'Gorman, and Gary W. Eck

Abstract: We compared predatory demand by pelagic planktivorous prey fish with invertebrate production in Lake Michigan during 1987 and in Lake Ontario during 1990. Predation by the planktivores in Lake Ontario was nearly fourfold higher than in Lake Michigan (approx. 87 g wet weight·m^{-2}·$year^{-1}$). Predation rates on *Mysis* were comparable in Lakes Michigan and Ontario (approx. 21 g·m^{-2}·$year^{-1}$), while predation on *Diporeia* was markedly higher in Lake Michigan than in Lake Ontario (21.3 vs. 8.5 g wet weight·m^{-2}·$year^{-1}$). In Lake Ontario, predatory demand on zooplankton exceeded our best estimate of production by a factor of 1.7. Similarly, predation estimates on Mysis in Lake Ontario were 1.2–2.0 times the estimated rate of production, depending on the production model used. Lake Michigan planktivores consumed approximately 55% of available zooplankton production in 1987, indicating that competition for prey resources, if operating, was not as intense as that in Lake Ontario in 1990. It is unclear how to resolve the paradox that predation could markedly exceed available prey production in some cases. There could be sources of error in the estimates of both the supply and demand sides of these trophic relationships.

Résumé : Nous avons comparé à la production d'invertébrés la demande prédatrice des poissons pélagiques planctivores servant eux-mêmes de proies, en 1987 dans le lac Michigan et en 1990 dans le lac Ontario. Dans ce dernier lac, la prédation par les planctivores était près de quatre fois plus élevée que dans le lac Michigan (environ 87 g poids frais·m^{-2}·an^{-1}). Les taux de prédation à l'égard des *Mysis* étaient comparables dans les deux lacs (environ 21 g·m^{-2}·an^{-1}), tandis que la prédation à l'égard des *Diporeia* était nettement plus haute dans le lac Michigan que dans le lac Ontario (21,3 contre 8,5 g poids frais·m^{-2}·an^{-1}). Dans le lac Ontario, la demande des prédateurs à l'égard du zooplancton dépassait d'un facteur de 1,7 notre meilleure estimation de la production. De même, les estimations de la prédation à l'égard des *Mysis* dans le lac Ontario correspondait à 1,2–2,0 fois le taux estimé de production, selon le modèle de production retenu. Les planctivores du lac Michigan ont consommé environ 55% de la production disponible de zooplancton en 1987, ce qui indique que la concurrence à l'égard des ressources en proies, si elle existait, n'était pas

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aussi intense que dans le lac Ontario en 1990. Comment expliquer le paradoxe qui fait que la prédation semble dans certains cas dépasser de façon marquée la production de proies disponibles? Il peut y avoir des sources d'erreurs dans les estimations tant de l'offre que de la demande dans ces relations trophiques.

[Traduit par la Rédaction]

Introduction

Planktivores and their invertebrate prey are an important link in the pelagic food web of the Great Lakes. Pelagic planktivores, and alewife (*Alosa pseudoharengus*) in particular, play important roles in supporting salmonine populations and in controlling and restructuring zooplankton and macroinvertebrate communities in the Great Lakes. Alewife have been implicated in controlling large-bodied zooplankton in Lake Michigan (Wells 1970; Evans 1990) and in Lake Ontario (Johannsson et al. 1991; O'Gorman et al. 1991); they were also important in reducing the mean size of zooplankton in Lake Michigan, particularly during the late 1960s when the alewife population reached a peak in abundance. A comparison of planktivore biomass (S.B. Brandt, Buffalo State College, Buffalo, N.Y., unpublished data) and mean sizes of zooplankton (Sprules and Goyke 1994) between Lakes Michigan and Ontario in recent years indicates that levels of planktivory in Lake Ontario are likely to be much higher than in Lake Michigan. In addition, the bloater (*Coregonus hoyi*), following a marked increase in its abundance in recent years, may be causing a decline of *Mysis* and *Diporeia* in Lake Michigan (McDonald et al. 1990).

Evidence for control of zooplankton and macroinvertebrates by planktivores have largely depended on correlations between time-series data sets of zooplankton abundance and species composition and indices of planktivore abundance based on trawl surveys (e.g., Evans 1990; Johannsson and O'Gorman 1991). It is apparent that top-down control can only be important if a substantial proportion of the annual prey production is consumed by predators. However, the level at which it becomes an important element in restructuring food web composition is difficult to ascertain without carefully controlled experiments. This question has been addressed in smaller lakes and ponds (Carpenter et al. 1985; Carpenter 1988), yet it is not feasible to carry out experiments of this nature on a system as large and spatially heterogeneous as the Great Lakes. We can, however, compare food web dynamics between lakes to help advance our understanding of the relative importance of planktivore predation in structuring the Great Lakes pelagic food webs.

Several studies have identified competition for limited food resources as an important mechanism affecting planktivores in Lake Michigan (Crowder et al. 1981; Crowder and Binkowski 1983; Crowder and Crawford 1984; Crowder 1986). These studies have concluded that alewife has outcompeted the indigenous planktivores for zooplankton resources. Crowder (1986) claims that the recent increase in abundance of bloater is a result of gill-raker and life-history adaptations that have enabled bloater to more effectively partition food resources and reduce resource competition with alewife. The support for this hypothesis has come largely from diet studies and food resource overlap measures. Shared resources are a necessary but not sufficient condition for exploitative competition to occur. We contend that for food resource competition to be operative, prey consumption by the planktivores should represent a substantial proportion of available prey production. That is, it must be demonstrated that food at some period becomes a limiting factor that adversely affects growth and, ultimately, fecundity or survival rates. The precise predation level at which competition becomes an important regulatory process is not clear, but comparing Lakes Ontario and Michigan provides a first indication of the relative intensities of resource limitation and, therefore, of the importance of competition for these resources.

To provide more compelling evidence of these assertions, we estimated lake-wide planktivore predation and compared that with independent estimates of prey production in both lakes. Tracking seasonal dynamics of predation and prey production may also help improve our understanding of the temporal nature of top-down control (e.g., Rudstam et al. 1992). Although the tools to construct a predator demand model have been in existence for some time (Ney 1990), some key empirical data, such as reliable estimates of lake-wide population abundance, have only recently been collected. Also, published data on zooplankton and macroinvertebrate production in the Great Lakes have been lacking or are dated and do not reflect recent ecosystem changes in the Great Lakes.

Our primary objective was to estimate prey consumption by the dominant pelagic planktivores in Lake Michigan in 1987 and Lake Ontario in 1990 and to compare consumption with independent data on invertebrate prey production. We use that information to test the hypothesis that planktivores require all the energy available through invertebrate prey production and that this predation pressure is greater in Lake Ontario given the higher observed biomass of planktivores and the clear signs of an intensively utilized zooplankton community.

To test the hypotheses, we formed the following objectives: (1) refine and implement existing bioenergetic models for alewife, bloater, and rainbow smelt (*Osmerus mordax*) in Lake Michigan and apply the alewife and rainbow smelt models, with appropriate site-specific data, to Lake Ontario; (2) summarize data on planktivore diets in Lakes Michigan and Ontario for input into the model; (3) estimate microcrustacean zooplankton production in Lake Ontario in 1990; (4) summarize recently published data on invertebrate production in both lakes; and (5) measure the effect of fish predation by comparing cumulative monthly and annual fish predation with invertebrate prey production.

Table 1. Wet weight diet composition of three age groups of alewife used in the bioenergetic model for Lake Michigan. Dietary proportions were based on literature values and from trawling surveys conducted in May and August–September of 1987, October 1988, and April 1989. Simulation day 1 is July 1.

Date	Simulation day	*N*	Wet weight diet composition						Source
			Mysis	*Diporeia*	Cladocerans	Copepods	*Bythotrephes*	Other[a]	
Young of the year									
Aug. 19	50		0.00	0.00	0.80	0.20	0.00	0.10	Hewett and Stewart 1989
Oct. 11	104	32	0.00	0.00	0.22	0.78	0.00	0.00	This study
Dec. 1	154		0.00	0.00	0.70	0.30	0.00	0.00	Hewett and Stewart 1989
Feb. 1	216	87	0.00	0.00	0.10	0.90	0.00	0.00	Hewett and Stewart 1989
Apr. 19	294	62	0.38	0.04	0.00	0.42	0.00	0.16	This study
May 25	330	133	0.01	0.35	0.00	0.30	0.00	0.34	This study
June 30[b]	365		0.01	0.35	0.00	0.30	0.00	0.34	This study
Yearlings									
July 1[c]	1		0.01	0.23	0.23	0.45	0.06	0.02	This study
Aug. 31	62	170	0.01	0.23	0.23	0.45	0.06	0.02	This study
Oct. 11	104	191	0.02	0.02	0.59	0.34	0.03	0.00	This study
Dec. 1[b]	154		0.02	0.02	0.59	0.34	0.03	0.00	Hewett and Stewart 1989
Feb. 1	216		0.00	0.06	0.07	0.87	0.00	0.00	Hewett and Stewart 1989
Apr. 19	294	82	0.31	0.50	0.00	0.19	0.00	0.00	This study
May 1	330	55	0.06	0.58	0.00	0.12	0.00	0.24	This study
June 30[c]	365		0.11	0.02	0.62	0.16	0.08	0.01	This study
Adults									
July 1[c]	1		0.11	0.02	0.62	0.16	0.08	0.01	This study
Aug. 31	62	168	0.11	0.02	0.62	0.16	0.08	0.01	This study
Oct. 11	104	31	0.63	0.00	0.21	0.03	0.13	0.00	This study
Jan. 1	185		0.15	0.30	0.35	0.20	0.00	0.00	Hewett and Stewart 1989
Feb. 1	216		0.15	0.40	0.10	0.35	0.00	0.00	Hewett and Stewart 1989
Apr. 19[d]	294		0.31	0.50	0.00	0.19	0.00	0.00	This study
May 25[d]	330		0.06	0.58	0.00	0.12	0.00	0.24	This study
June 30[d]	365		0.11	0.02	0.62	0.16	0.08	0.01	This study

[a]Other = rotifers (alewife larvae) and mostly chironomids, ostracods, fingernail clams, fish eggs, and insects (alewife YOYs and older).
[b]Values for this day taken from values for start day of interval immediately prior.
[c]Values for this day taken from values for start day of interval immediately following.
[d]Because of difficulty in distinguishing between yearlings and adults in some samples, we applied the same diet composition values for adults from the corresponding days in the yearling age group.

Methods

Bioenergetic models

We implemented existing bioenergetic models for alewife (Stewart and Binkowski 1986; Hewett and Stewart 1989), rainbow smelt (Lantry and Stewart 1993), and bloater (Rudstam et al. 1994) to simulate predation in Lakes Michigan and Ontario. All the planktivore models were implemented using the program of Hewett and Johnson (1992). The bioenergetic parameters developed for these species appear in the above publications and are, therefore, not included in the present paper. We implemented the conservative larval alewife model (model A of Hewett and Stewart 1989) to simulate predation by larvae of this species in both lakes. We refer the reader to Lantry and Stewart (1993) for a description of the development of the rainbow smelt model in Lakes Michigan and Ontario. Our results using their model differ marginally from those previously reported based on some different assumptions about prey energy density (see Predator and prey energy density in the Methods section). Below we present the site-specific data input into the models for alewife and bloater and present the methods to estimate available invertebrate prey production.

Planktivore diets

Lake Michigan

Diet data for alewife, bloater, and rainbow smelt were obtained from a field study carried out in Lake Michigan during 1987–1989. Samples of fish were collected in midwater and bottom trawls as part of a lake-wide assessment of planktivore abundance. The samples were collected across the lake corresponding to the sampling transects reported by Brandt et al. (1991). We included day and night samples to account for diel dynamics of planktivore predation. We examined stomach contents from alewife collected at each transect site in May and August–September 1987, October 1988, and April 1989. We summarized data on bloater diets from collections at each transect site in May 1987 and from the Ludington, Mich., and Two Rivers, Wis., sites in August–September 1987.

Table 2. Wet weight diet composition by age group for bloater used in the bioenergetic model for Lake Michigan. Dietary proportions were based in part on fish collected with bottom and midwater trawls in spring and late summer 1987. Diet composition values during the fall and winter periods were interpolated between empirical estimates from Sept. 1 to May 25. Simulation day 1 is Oct. 1.

Date	Simulation day	*N*	Wet weight diet composition					Source
			Mysis	*Diporeia*	Cladocera	Copepods	Other[a]	
Larvae and young of the year								
July 1	274		0.00	0.00	0.01	0.98	0.01	Crowder and Crawford 1984
Aug. 1	305		0.00	0.00	0.17	0.83	0.00	Warren and Lehman 1988
Sept. 1	336		0.00	0.00	0.97	0.03	0.00	Warren and Lehman 1988
Yearlings								
May 25	237	163	0.04	0.23	0.00	0.59	0.15	This study
Aug. 31	335	290	0.26	0.27	0.18	0.26	0.03	This study
Age 2								
May 25	237	194	0.09	0.80	0.00	0.05	0.07	This study
Aug. 31	335	80	0.80	0.17	0.02	0.00	0.01	This study
Age 3 and older								
May 25	237	99	0.12	0.81	0.00	0.00	0.06	This study
Aug. 31[b]	335		0.80	0.17	0.02	0.00	0.01	This study

[a]Other = rotifers (bloater larvae) and mostly chironomids, ostracods, fingernail clams, fish eggs, and insects (bloater yearlings and older).
[b]Diet proportions during this period were taken from corresponding age 2 period.

The fish were preserved in 10% formalin immediately following capture. Stomachs were extracted and contents were removed and placed on a 12-cm-diameter gridded Petri plate under a dissecting scope (20× power). Based on the number of organisms in the subsample, either the whole sample or some fraction (typically one quarter to one half) was enumerated. Total number of prey items were estimated from subsample counts by direct proportion.

Prey items found in alewife stomachs were identified into the following general taxonomic categories: *Mysis relicta*, *Diporeia hoyi*, small cladocerans (mostly *Bosmina*, *Eubosmina*, and *Ceriodaphnia*), large cladocerans (mostly *Daphnia*), copepods, *Bythotrephes cederstroemi*, and other (mostly chironomids, oligochaetes, and terrestrial insects; Table 1). In spring (April and May), alewife often had a dense bolus of *Bythotrephes* spines in their stomach (described by Keilty 1990). We hypothesize that these spines had a prolonged residence time in the gut given the reduced availability of *Bythotrephes* to foraging alewife during April and May in Lake Michigan (Evans 1988; Sprules et al. 1990). Therefore, we determined the number of recently ingested *Bythotrephes* in the stomach by counting other body parts. Diet data for Lake Michigan alewife during the larval and yearling and adult winter periods were taken from Hewett and Stewart (1989).

We included five diet categories for bloaters in Lake Michigan: *Mysis*, *Diporeia*, cladocerans, copepods, and other (rotifers for larvae; chironomids, ostracods, fingernail clams, fish eggs and insects for older age classes; Table 2). *Bythotrephes* was a rare prey item in the diets of bloaters in 1987 and were not included as a separate prey category. Insufficient numbers of young-of-year bloater were collected during the late summer survey to characterize their diet in 1987. We relied on two published sources of Lake Michigan young-of-the-year bloater diets to represent diet composition for this age group in the model. Crowder and Crawford (1984) published values of diet composition for young-of-the-year (YOY) bloater during July and August 1982 and 1983, and Warren and Lehman (1988) published values for YOY diets during August and September of 1985 and 1986. It was apparent in both studies that YOY bloater exhibit an ontogenetic shift in diet from small cyclopoid copepods to larger daphnids at a size of approximately 30–35 mm total length (TL). We applied Crowder and Crawford's (1984) data for July and Warren and Lehman's (1988) data for August and September in the bloater model for Lake Michigan (Table 2).

Lake Ontario

To implement the bioenergetic model for Lake Ontario alewife, we used the diet data of Hewett and Stewart (1989) for larval alewife, Urban and Brandt (1993) for YOY alewife, and Mills et al. (1992) for yearling and adult alewife. Urban and Brandt (1993) summarized the diet of YOY alewife collected night and day with midwater trawls during the fall of 1984 and 1986 in southeastern Lake Ontario. Mills et al. (1992) collected alewife with bottom trawls in the daytime during April–October 1988 at ports along the New York shoreline of Lake Ontario. They found a high incidence of *Bythotrephes* in the diet of alewife during 1988 based on spine counts. During 1990, *Bythotrephes* were rare in net samples (O. Johannsson, personal observation) and in alewife stomachs (R. O'Gorman, personal observation). Therefore, we removed *Bythotrephes* from the diet data of Mills et al. (1992) and recalculated wet weight fractions of the diet based on the relative proportions of the remaining prey categories (Table 3).

Table 3. Wet weight diet composition by four age groups of alewife as used in the bioenergetic model for Lake Ontario. Simulation day 1 is July 1.

Date	Simulation day	*N*	Wet weight diet composition					Source
			Mysis	*Diporeia*	Cladocera	Copepods	Other[a]	
Young of the year								
Aug. 19[b]	50		0.00	0.00	0.26	0.74	0.00	Urban and Brandt 1993
Aug. 22	53	15	0.00	0.00	0.26	0.74	0.00	Urban and Brandt 1993
Oct. 1	93	20	0.00	0.00	0.54	0.74	0.00	Urban and Brandt 1993
Oct. 26	118	87	0.00	0.00	0.32	0.68	0.00	Urban and Brandt 1993
Nov. 13	136	42	0.00	0.00	0.40	0.60	0.00	Urban and Brandt 1993
Feb. 1	216		0.00	0.00	0.10	0.90	0.00	Hewett and Stewart 1989
May 1	305	31	0.00	0.00	0.00	1.00	0.00	Mills et al. 1992
June 8	343	56	0.00	0.00	0.08	0.92	0.00	Mills et al. 1992
June 30[b]	365		0.00	0.00	0.40	0.60	0.00	Mills et al. 1992
Yearlings								
July 1[b]	1		0.00	0.00	0.40	0.60	0.00	Mills et al. 1992
July 25	25	14	0.00	0.00	0.40	0.60	0.00	Mills et al. 1992
Sept. 15	77	32	0.07	0.01	0.25	0.57	0.10	Mills et al. 1992
Oct. 23	115	143	0.31	0.00	0.53	0.13	0.01	Mills et al. 1992
Dec. 1[c]	154		0.31	0.00	0.53	0.13	0.01	Mills et al. 1992
Feb. 1	216		0.00	0.06	0.07	0.87	0.00	Hewett and Stewart 1989
May 1	305	120	0.35	0.16	0.02	0.44	0.03	Mills et al. 1992
June 8	343	105	0.06	0.16	0.07	0.70	0.01	Mills et al. 1992
June 30[b]	365		0.00	0.00	0.22	0.63	0.01	Mills et al. 1992
Adults								
July 1[b]	1		0.00	0.00	0.22	0.63	0.01	Mills et al. 1992
July 25	25	162	0.00	0.00	0.22	0.63	0.01	Mills et al. 1992
Sept. 15[d]	77		0.07	0.01	0.25	0.57	0.10	Mills et al. 1992
Oct. 23[d]	115		0.31	0.00	0.53	0.13	0.01	Mills et al. 1992
Jan. 1	154		0.15	0.30	0.35	0.20	0.00	Hewett and Stewart 1989
Feb. 1	216		0.15	0.40	0.10	0.35	0.00	Hewett and Stewart 1989
May 1[d]	305		0.35	0.16	0.02	0.44	0.03	Mills et al. 1992
June 8[d]	343		0.06	0.16	0.07	0.70	0.01	Mills et al. 1992
June 30[d]	365		0.00	0.00	0.22	0.63	0.01	Mills et al. 1992

[a]Other = rotifers (alewife larvae) and mostly chironomids, ostracods, fingernail clams, fish eggs, and insects (alewife YOY, yearlings, and adults).

[b]Values for this day taken from values for start day of interval immediately following.

[c]Values for this day taken from values for start day of interval immediately prior.

[d]Because of difficulty in distinguishing between yearlings and adults in some samples, we applied the same diet composition values for adults from the corresponding days in the yearling age group.

Planktivore abundance and population model development

To implement an age-structured simulation of the planktivore populations in both lakes, we partitioned acoustic estimates of lake-wide biomass for each planktivore species into biomass of separate age-classes. Methods used to calculate lake-wide biomass and abundance by sampling lake transects using acoustics can be found elsewhere (Brandt et al. 1991; Goyke and Brandt 1993). Below we present methods to estimate age-specific biomass for the alewife and bloater populations.

We developed a hypothetical bioenergetic simulation of 1000 individuals in the alewife and bloater populations. The first day of the simulation corresponded to the approximate date of the trawl surveys conducted in each lake (Lake Michigan National Biological Survey (NBS) trawl assessment, October 1, 1987; Lake Ontario NBS and New York State Department of Environmental Conservation (NYDEC) trawl assessment, May 1, 1990). The total numbers in the hypothetical population were partitioned into each age-class (age ≥1+) using age-specific annual mortality rates based on the NBS surveys (see Tables 4, 5, and 6 for values and sources of mortality parameters for each species). The bioenergetic model of Hewett and Johnson (1992), which accounted for both individual growth and age-specific mortality of the population, was used to project biomass composition of the population by age on the day of the acoustic surveys (September 1 for Lake Michigan, Brandt et al. 1991; November 1 for Lake Ontario, Goyke and Brandt 1993). These estimated proportions were then multiplied by the acoustic biomass estimates for the populations to approximate age-specific

biomass on the approximate median day of acoustic lake sampling.

We then back calculated abundance for each age-class to the first day of the bioenergetic simulation for both species. Abundance of yearling and older fish on July 1 (alewife) and October 1 (bloater) was estimated using the survival values reported in Tables 4, 5, and 6. Below we present the methods used to back calculate young of year abundances prior to July 1 for alewife and prior to October 1 for bloater.

The acoustic survey in Lake Michigan did not include estimates of YOY alewife abundance because YOY on September 1 were too small to be sampled accurately (Brandt et al. 1991). We back calculated abundances of larvae and YOY alewife from observed yearling abundances using published estimates of survival during these periods (Mansfield and Jude 1986; Hewett and Stewart 1989; Table 4). For Lake Michigan bloater, we assumed that the observed mortality rates (October 1, 1986, to October 1, 1987) for age 1 to age 2 fish were also valid for age 0 on September 1 to age 1 on October 1 (Table 5). We used these mortality rates to estimate YOY abundance on September 1. We then multiplied this value by the mean weight at age of YOY on September 1 (Rudstam et al. 1994) to estimate YOY biomass. We estimated YOY bloater abundance and mortality between July 1 and September 1 as follows. Bloater larvae hatch in the hypolimnion and move to the surface (Rice et al. 1987). Abundance of 20 mm (0.030 g) larvae in the top 0.1 m of water ranged from 2500 to 8300 fish·ha^{-1} for 1982, 1983, 1984, and 1986 (average 5100 from samples over six different water depths along a transect off Milwaukee, Wis.; J. Rice, North Carolina State University, Raleigh, unpublished data). This density may be representative of the top 0.5 m (Nash and Geffen 1991), resulting in an average abundance of 25 500 fish·ha^{-1} on July 15. Nash and Geffen (1991) measured densities of 15 000 fish·ha^{-1}. The data of Rice et al. (1987; J. Rice, unpublished data) are admittedly an inexact estimate of mortality rates of larvae because of the changes in the vulnerability of larvae to neuston nets. However, these data are the best available. Daily instantaneous mortality rates during the most vulnerable period (around 20-mm size) ranged between 0.0821 and 0.0984. We used the average value of 0.0885 as our present best estimate of larval mortality between first feeding larvae (July 1, 0.0083 g) and 20 mm (July 15, 0.030 g). Mortality between July 1 and September 1 was then calculated assuming a logarithmic decline in abundance using our assumed bloater densities on July 15 (25 500 fish·ha^{-1}) and September 1 (3150 fish·ha^{-1}, based on acoustic estimate of Brandt et al. (1991) and the procedure outlined above; Table 5).

Young-of-the-year alewife were large enough to provide direct acoustic measures of lake-wide abundance and biomass in Lake Ontario. We used this estimate with the back-calculated estimate of yearling alewife abundance on July 1 (derived above) to generate mortality values over the winter and early spring period (November 1 – May 1; Table 6). The estimated instantaneous mortality rate (0.007 637) was also applied to YOY over the month of October (Table 6). We then estimated YOY and larvae abundance prior to October 1 using mortality rates reported for Lake Michigan YOY alewife (Mansfield and Jude 1986; Hewett and Stewart 1989; Table 6).

Planktivore growth

Weights of Lake Michigan alewife larvae input into the model were taken from Hewett and Stewart (1989). We subdivided the model age 1 cohort of Hewett and Stewart (1989) into three separate intervals (simulation days 50–92, 93–329, 330–365, where day 1 = July 1), which allowed us to constrain the first year of growth with empirical estimates of alewife weight at age measured during 1987. The estimate on simulation day 93 (October 1) was the measured mean weight of YOY alewife collected as part of the NBS trawl assessments in 1986 and 1987. We also included an estimate for yearling wet weight on simulation day 330 (May 24, 1987) based on samples (N = 36) collected from midwater and bottom trawls in Lake Michigan on that date (Brandt et al. 1991). For subsequent modeled age groups (age ≥1) we applied the seasonal growth dynamics described in Stewart and Binkowski (1986) based on the original data of Flath and Diana (1985). We adjusted the growth parameters of Stewart and Binkowski (1986) for the fall period (simulation day 76 for yearlings and simulation day 119 for older age groups) until predicted weight on October 1 was within 1% of observed mean weights in the 1986 and 1987 NBS trawl assessments (Table 4).

For Lake Michigan bloater, we used an annual simulation period (Rudstam et al. 1994) based on weight-at-age estimates from the fall NBS trawl assessment for YOY bloater (beginning on October 1) and older age groups (Table 5). Growth data prior to October 1 for YOY bloater were obtained from sampling in September 1987 (Brandt et al. 1991) and earlier data from Rice et al. (1987; J. Rice, unpublished data; Table 5).

For Lake Ontario alewife, we applied the larval weights of Lake Michigan alewife reported in Hewett and Stewart (1989; Table 6). The first year of life for post-larval alewife (from YOY on August 19 to yearlings on July 1) was divided into four separate modeled intervals. Starting and ending times of these growth periods corresponded to the days of trawl sampling described by Rand et al. (1994). The sampling dates were September 13 and November 2, 1989 (YOY), and May 2 and July 7, 1989 (yearlings; Table 6). For yearlings (after July 1) and older alewife, we converted total length at age measured in May 1990, during the NBS/NYDEC trawl assessment to wet weight based on the length–weight parameters reported in Rand et al. (1994). Because our simulations began on July 1, we increased weight at age measured in May by 9% to estimate weight on July 1 for all alewife age ≥1. This was based on the ratio of age 2 alewife collected on July 7, 1989, to age 2 alewife collected in early May 1990, in the NBS/NYDEC trawl survey.

Weight of age 1 and older alewife in Lake Ontario in the fall of 1990 (November 1 in the model) was estimated by applying the mean lengths of each cohort in spring 1991 in the length–weight regressions calculated from data collected during the fall of 1990 (R. O'Gorman, unpublished

Table 4. Population abundance, biomass, mean weights, and mortality parameters for alewife in Lake Michigan during 1987.

Cohort	Age group	Calendar date	Simulation day	Mean weight (g)	Population number (millions)	Population biomass (thousands of tonnes)	Daily instantaneous mortality
1	Larvae	July 11	11	0.000 13[a]	277 904	0.04	0.046 545[c]
2	YOY	Aug. 19	50	0.16[a]	43 122	6.9	0.037 429[d]
3	YOY	Oct. 15	107	4.2	7 610	31.96	0.005 238[d]
4	Yearling	May 24	330	5.1[b]	2 175	11.09	0.005 238[d]
5	Yearling	July 1	1	7.66	2 064	15.81	0.005 591[d]
6	Yearling	Aug. 19	50	12.55	1 561	19.6	0.005 591[d]
7	Yearling	Sept. 14	76	16.84	1 349	22.7	0.005 591[d]
8	Yearling	Oct. 1	93	17.5			0.002 577[d]
9	Age 2	May 27	324	11.63	677	7.9	0.002 577[d]
10	Age 2	July 1	1	21.19	659	14	0.002 577[d]
11	Age 2	Aug. 19	50	20.45	579	11.8	0.002 577[d]
12	Age 2	Oct. 1	93	29.5			0.002 592[d]
13	Age 2	Oct. 27	119	30.08	485	14.6	0.002 592[d]
14	Age 3	June 16	351	31.99	266	8.5	0.002 592[d]
15	Age 3	July 1	1	31.26	257	8	0.002 592[d]
16	Age 3	Aug. 19	50	29.41	226	6.6	0.002 592[d]
17	Age 3	Oct. 1	93	41			0.001 855
18	Age 3	Oct. 27	119	41.93	192	8.1	0.001 855
19	Age 4	June 16	351	41.11	125	5.1	0.001 855
20	Age 4	July 1	1	40.02	122	4.9	0.001 855
21	Age 4	Aug. 19	50	36.75	111	4.1	0.001 855
22	Age 4	Oct. 1	93	51.5			0.002 826
23	Age 4	Oct. 27	119	50.77	96	4.8	0.002 826
24	Age 5	June 16	351	45.41	50	2.3	0.002 826
25	Age 5	July 1	1	43.98	46	2	0.002 826
26	Age 5	Aug. 19	50	40.5	40	1.6	0.002 826
26	Age 5	Oct. 1	93	56.5[a]			0.002 356
27	Age 5	Oct. 27	119	56.17	34	1.9	0.002 356
28	Age 6	June 16	351	50.83	19	1	0.002 356
29	Age 6	July 1	1	49.27	19	0.9	0.002 356
30	Age 6	Aug. 19	50	44.7	17	0.8	0.002 356
30	Age 6	Oct. 1	93	62.5[a]			0.006 308
31	Age 6	Oct. 27	119	60.75	13	0.8	0.006 308
32	Age 7	June 16	351	51.53	3	0.2	0.006 308

Note: Mean weights (in October for YOYs and older) and mortality of older age groups (after October 1 of third year of life) are based on catches in the standard bottom trawl survey by the NBS in the fall of 1986 and 1987 (average day of capture = October 1). Mean weights at other points during the year were estimated based on the seasonal growth pattern described for Lake Michigan. Cohort refers to the modeled interval defined by an initial and final empirical weight. Population number and biomass were based on an acoustic biomass estimate on September 1, 1987. Simulation day 1 is July 1.

[a]Weight from Hewett and Stewart (1989).

[b]Mean weight from trawl-caught YOY alewife in late May in Lake Michigan (Brandt et al. 1991).

[c]From Mansfield and Jude (1986).

[d]From Hewett and Stewart (1989).

data). This resulted in each age-class, beginning with yearlings on July 1, having three separate modeled intervals with weights input on July 1 (simulation day 1), November 1 (simulation day 125), and May 1 (simulation day 306) of the following year. From all the weight data (Table 6) we estimated the mean growth trajectories (based on empirical weights and model interpolations) of the dominant planktivore species in both lakes (Fig. 1).

Predator and prey energy density

We used data from Rand et al. (1994) to represent the seasonal dynamics of energy density of alewife in both lakes. The Lake Michigan data were a composite of samples collected near Two Rivers, Wis., in January, February, and March, 1986, and samples collected in May and September, 1987, off the ports of Ludington, Mich., Two Rivers and Sturgeon Bay, Wis., and Waukegon, Ill. The data for Lake

Table 5. Population abundance, biomass, mean weights, and mortality parameters for bloater in Lake Michigan during 1987.

Cohort	Age group	Calendar date	Simulation day	Mean weight (g)	Population number (millions)	Population biomass (thousands of tonnes)	Daily instantaneous mortality
1	Larvae	July 1	274	0.0083	653 000	5.4	0.088 50
2	Larvae	July 15	291	0.03	145 000	4.4	0.045 45
3	YOY	Oct. 1	1	2.6	16 645	43.8	0.002 46
4	Yearling	Oct. 1	1	15.2	6 772	102.9	0.002 46
5	Age 2	Oct. 1	1	34.6	2 755	95.4	0.002 46
6	Age 3	Oct. 1	1	64.1	1 121	71.8	0.002 97
7	Age 4	Oct. 1	1	96.8	382	37	0.003 50
8	Age 5	Oct. 1	1	125.7	108	13.6	0.004 15
9	Age 6	Oct. 1	1	152.6	23	3.5	0.004 71

Note: Derivation of mean weights and mortality of larvae and juveniles is described in text. Mean weights and mortality of older age groups (yearlings and older) are based on catches in the standard bottom trawl survey by the NBS in fall, 1986 and 1987 (average day of capture = October 1). Population numbers and biomass of YOY and older bloater were based on an acoustic estimate on September 1, 1987. Simulation day 1 is Oct. 1.

Ontario were based on samples collected in a monthly trawl survey conducted from April to October 1989 and March 1990 at a site off Oswego, N.Y. Energy density of bloater in Lake Michigan was based on a predictive regression of energy density and body size (Rudstam et al. 1994).

We included seasonal values of *Mysis* and *Diporeia* energy density in the planktivore models based on data that appear in Gardner et al. (1985). We calculated energy content of lipid and nonlipid (protein and carbohydrate) reserves in the macroinvertebrates assuming a caloric content of 38.9 J·mg^{-1} and 17.2 J·mg^{-1}, respectively (Gardner et al. 1985). We estimated wet weights based on the ash-free dry weight / dry weight ratio of 0.87 for *Diporeia* and 0.92 for *Mysis* (Gardner et al. 1985) and dry weight / wet weight ratios of 0.26 for *Diporeia* and 0.16 for *Mysis* (Hewett and Johnson 1992). We averaged the energy density values for the separate collections of *Diporeia* at two depths (29 and 45 m). Wet weight energy density in *Diporeia* was found to cycle strongly with a peak in July (6022 J·g wet weight (wt)$^{-1}$) and a seasonal low in April (4867 J·g wet wt^{-1}). *Mysis* exhibited less pronounced fluctuations, with a peak in June and July (3712 J·g wet wt^{-1}), and a seasonal low in April (3361 J·g wet wt^{-1}). Because of a lack of data on energy density of Lake Ontario macroinvertebrates, we implemented these data in growth simulations for both lakes. We assumed energy density of cladocerans (including *Bythotrephes*) to be 1674 J·g wet wt^{-1} and copepods to be 2302 J·g wet wt^{-1} as reported elsewhere (Hewett and Stewart 1989; Lantry and Stewart 1993).

Evaluation of bioenergetic model sensitivity

We evaluated the sensitivity of the model to a number of different inputs. Because physiological parameter sensitivities have been comprehensively evaluated on a similar model (Bartell et al. 1986), we chose to evaluate the importance of swimming speed and some of the key site-specific empirical inputs. We conducted individual parameter perturbations (IPP, ±10% of nominal) on the following: swimming speed, survival parameters, population abundance, individual growth data, and occupied water temperature. We measured the deviation in model estimates of lake-wide consumption by bloater in Lake Michigan and alewife in Lakes Michigan and Ontario. Sensitivity analysis was not carried out on rainbow smelt based on their small contribution to total planktivore predation (see Lantry and Stewart 1993 for results of a similar sensitivity analysis on this species).

Zooplankton and macroinvertebrate production

We used estimates of zooplankton production in Lake Michigan during 1987 reported by Sprules et al. (1991). In addition, we relied on various other published sources of macroinvertebrate production (*Mysis* and *Diporeia*) in Lake Michigan estimated during the 1970s and 1980s (Lubner 1979; Sell 1982; Gardner et al. 1985).

We estimated production of microcrustacean zooplankton in Lake Ontario during 1990 based on weekly sampling (April–October) of the surface waters (0–20 m when not stratified or stratified to depths >20 m, mixed depth minus 1 m when stratified) at two stations (mid-lake and Kingston Basin). Samples were collected from a metered 64-μm mesh net with abundances corrected for net efficiency. Diel vertical distributions of zooplankton indicate that daytime sampling may greatly underestimate the population of *Diacyclops*, especially the adults when the system is stratified. Because production estimates are based on the egg ratio method, which requires accurate estimates of densities, the production of *Diacyclops* is greatly underestimated. The average percentage of adult *Diacyclops* occurring in the epilimnion during the day during the stratified period in 1990 was 31% at station 41 and 23% at station 81. Therefore, the production of *Diacyclops* was multiplied by 3 at station 41 and by 4 at station 81 for July, August, and the first half of September. We estimated production over the

Table 6. Population abundance, biomass, mean weights, and mortality parameters for alewife in Lake Ontario during 1990.

Cohort	Age group	Calendar date	Simulation day	Mean weight (g)	Population number (millions)	Population biomass (thousands of tonnes)	Daily instantaneous mortality
1	Larvae	July 11	11	0.000 13[a]	1 278 575	0.17	0.046 545[c]
2	YOY	Aug. 19	50	0.16[a]	198 681	31.79	0.037 429[d]
3	YOY	Sept. 1	76	0.39[b]	72 321	28.21	0.037 429[d]
3	YOY	Oct. 1	93		36 869		0.007 637[e]
4	YOY	Nov. 1	125	4.04[b]	28 438	114.89	0.007 637[e]
5	Yearling	May 1	306	5.65	7 083	40.02	0.004 409
6	Yearling	July 1	1	7.99[b]	5 437	43.44	0.004 409
7	Yearling	Nov. 1	125	18.18	3 133	56.96	0.004 409
8	Age 2	May 1	306	16.07	1 404	22.56	0.000 445
9	Age 2	July 1	1	17.5	1 367	23.92	0.000 445
10	Age 2	Nov. 1	125	24.1	1 293	31.16	0.000 445
11	Age 3	May 1	306	20.69	1 193	24.68	0.000 445
12	Age 3	July 1	1	21.02	1 161	24.4	0.000 445
13	Age 3	Nov. 1	125	26.1	1 098	28.66	0.000 445
14	Age 4	May 1	306	23.3	1 013	23.61	0.000 445
15	Age 4	July 1	1	23.2	986	22.88	0.000 445
16	Age 4	Nov. 1	125	28	933	26.12	0.000 445
17	Age 5	May 1	306	27.6	860	23.74	0.001 638
18	Age 5	July 1	1	26.8	780	20.9	0.001 638
19	Age 5	Nov. 1	125	30.7	635	19.5	0.001 638
20	Age 6	May 1	306	30.75	472	14.51	0.002 876
21	Age 6	July 1	1	29.47	397	11.7	0.002 876
22	Age 6	Nov. 1	125	33	277	9.1	0.002 876
23	Age 7	May 1	306	30.21	164	4.95	0.003 299
24	Age 7	July 1	1	29.1	135	3.93	0.003 299
25	Age 7	Nov. 1	125	32.91	89	2.93	0.003 299
26	Age 8	May 1	306	34.12	49	1.67	0.003 299

Note: Unless otherwise noted, mean weights in May and July and mortality are based on catches in the standard bottom trawl survey by the NBS in the spring of 1990. Mean weights on November 1 for yearling and older fish were calculated based on lengths measured in the spring of 1991 (see text for details). Population number and biomass are based on the acoustic estimate for November 1, 1990. Simulation day 1 is July 1.

[a]Weights taken from Hewett and Stewart (1989).

[b]Weights obtained from a seasonal trawl survey conducted off Oswego in 1989 (Rand et al. 1994).

[c]Data from Mansfield and Jude (1987).

[d]Mortality rate from Hewett and Stewart (1989).

[e]Mortality estimated based on fitting logarithmic function to abundance data on YOYs (acoustic estimate on November 1, 1990) and yearlings (on May 1, back calculated from acoustic estimate of yearlings on November 1, 1990, using a yearling mortality estimate based on NBS bottom trawls).

entire calendar year of 1990 by assuming that daily production in November equaled 60% of that in October and production during December to March equaled that observed in April.

We also include estimates of Lake Ontario *Mysis* production and mortality in 1990 based on a bioenergetic model developed by Rudstam (1989). Methods and assumptions made in model development are included in Johannsson et al. (1994) except for temperature, which was modeled as mean monthly hypolimnetic temperature (Johannsson 1992), for loss rates; which changed with depth; and for total abundance, which was corrected for a net efficiency of 87% (Nero and Sprules 1986). A range of production estimates were calculated for the nearshore (50–100 m depth) and offshore (>100 m depth) at low (0.004 00·d^{-1}), medium (0.010 06·d^{-1}) and high (0.020 12·d^{-1}) daily instantaneous mortality rates of mysids >13.5 mm in length. Production in each region was then summed to provide whole lake estimates. A value for *Mysis* production calculated using the cohort method was also included in the analysis (Johannsson, 1995). Estimates for *Diporeia* production in Lake Ontario were taken from Johannsson (1985).

Results

Annual lake-wide predation by the planktivore community

Modeling results indicate that total predation on invertebrates was 3.9 times higher per unit area in Lake Ontario in 1990 than in Lake Michigan in 1987 (Table 7). Planktivory (including only consumed microcrustacean zooplankton) was much higher in Lake Ontario compared with Lake Michigan, whereas rates of benthivory (predation on *Mysis* and *Diporeia*) in both lakes were more comparable (Table 7). Predation rates on *Mysis* were similar in both lakes, while predation rates on *Diporeia* were markedly higher in Lake Michigan than in Lake Ontario (Table 7). Although the surface area of Lake Ontario is approximately one third that of Lake Michigan, total lake-wide predation was greater in Lake Ontario (6322 kt·year^{-1}) than in Lake Michigan (5037 kt·year^{-1}).

Predation per unit surface area in Lake Ontario exceeded that for Lake Michigan during every month of the year (Fig. 2). The amplitude of the predation cycle was much greater in Lake Ontario, owing to the pronounced seasonal cycle of growth and consumption in alewife and significantly higher prey fish densities. Although predation rates in both lakes were comparable in May, by October predation in Lake Ontario exceeded that in Lake Michigan by approximately sixfold (Fig. 2).

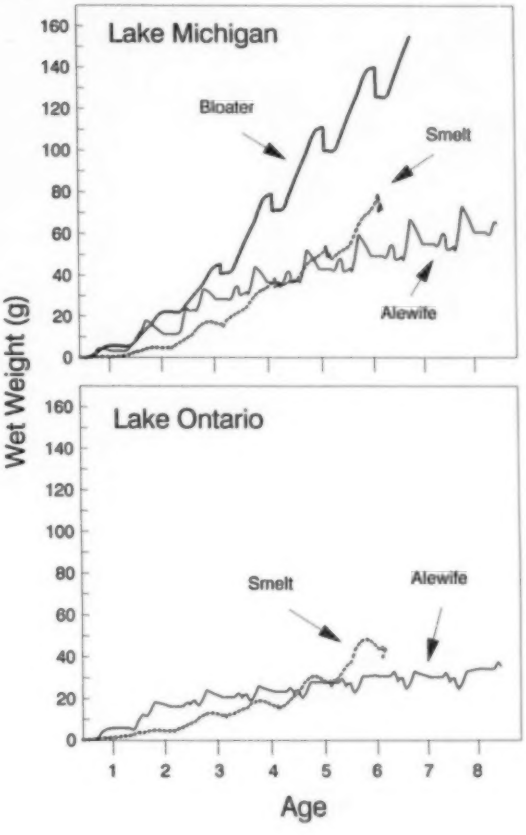
Lake-wide predation by planktivore population and by diet type

Bloater dominated predation in Lake Michigan, accounting for 68% of total predation (by wet weight) during 1987. Lake Michigan alewife were responsible for 28% of total lake-wide predation, and rainbow smelt were responsible for 4% (Fig. 3). In Lake Ontario, alewife accounted for over 96% of total predation on invertebrates during 1990. Because rainbow smelt accounted for such a small proportion of planktivore predation in both lakes and the results of bioenergetic simulations has been reported elsewhere (Lantry and Stewart 1993), we will focus here only on results for bloater and alewife.

Bloater and alewife have different seasonal patterns of predation. Owing to differences in growth schedules, the seasonal dynamics of predation were more pronounced for alewife than for bloater. The amplitude of the seasonal cycle of predation, measured as the ratio of the predation rate at the seasonal peak (in the fall) and the trough (in the spring), was 17.7 for Lake Michigan alewife and only 4.8 for Lake Michigan bloater (Figs. 4 and 5). The seasonal high occurred during August for the bloater population and September for the alewife population. The mean annual ratio of predation by larvae and YOY to total predation by the population was much higher for alewife (0.45) than bloater (0.23) in Lake Michigan (Figs. 4 and 5). Larvae and YOY alewife in Lake Ontario contributed the greatest proportion (0.47) to annual prey consumption of all the modeled populations (Fig. 6).

Mysis represented a significant proportion of annual wet weight prey consumption by bloater (30%), whereas *Mysis* contributed only a small proportion to the diets of alewife in Lake Michigan (7%) and Lake Ontario (7%;

Fig. 1. Simulated growth trajectories for the dominant pelagic planktivores in Lakes Michigan (top panel) and Ontario (bottom panel). Growth was simulated using a bioenergetic model and was constrained by inputs of empirical weights at age.



Figs. 4–6). The diet of alewife in both lakes consisted mostly of microcrustacean zooplankton, with minor seasonal peaks in consumption of *Diporeia* (spring) and *Mysis* (fall; Figs. 4 and 6). Bloater, conversely, exhibited a more protracted pattern of planktivory and maintained a relatively high rate of consumption on *Diporeia* and *Mysis*. There was a clear seasonal dynamic of prey consumption that closely resembled the pattern in alewife described above (Fig. 5). The seasonal pattern of predation by Lake Ontario alewife was similar to that of Lake Michigan alewife (Figs. 4 and 6), owing to the similar growth trajectories input into the model. Copepods made up a larger proportion of the zooplankton consumed by alewife in Lake Ontario (61%) than in Lake Michigan (49%). The rate of consumption on *Bythotrephes* in Lake Michigan was estimated at 0.9 g·m^{-2}·year^{-1}. *Bythotrephes* accounted for only a relatively small proportion of the annual food consumed by alewife in 1987 (4%: Lake Michigan, all age classes combined). This estimate is based on the diet formulation that included only whole body counts (see Planktivore Diets in Methods section).

Table 7. Summary of invertebrate production and planktivore predation (wet weights) in Lakes Michigan and Ontario.

Prey taxa	Production		Predation		Predation/production ratio
	$g \cdot m^{-2} \cdot year^{-1}$	$kt \cdot year^{-1}$	$g \cdot m^{-2} \cdot year^{-1}$	$kt \cdot year^{-1}$	
Lake Michigan					
Mysis	11.3–21.3[a]	942.1	21.2	1226.8	1.3
Diporeia	3.0–23.1[b], 14.0[c]	780.3	21.3	1228.5	1.6
Zooplankton	72.1–91.6[d]	4730.9	44.7	2582	0.6
Total		6453.3	87.2	5037.3	0.8
Lake Ontario					
Mysis	2.3–22.2[e]	205.1	21.8	403.2	1.2–2.0
	0.13–48.8[f]	337.9			
Diporeia	11.3[g]	208.8	8.5	156.4	0.8
Zooplankton	179.6–182.9[h]	3339.1	311.6	5792.1	1.6–1.7
	196.0–198.1[i]	3634.0			
Total		3842.8	341.9	6321.6	1.7

Note: In cases where more than one estimate for prey production was available, we present the range of values reported. The means of the highest and lowest production values were expanded to the whole lake based on lake surface areas (Lake Michigan, 5.78×10^{10} m^2; Lake Ontario, 1.82×10^{10} m^2). In the case of Lake Ontario *Mysis* and zooplankton production, whole-lake production was summed over a series of depth ranges, each characterized by different production rates. Planktivore predation includes all modeled species.

[a]Data from Sell (1982). Data from stations ranging from 50–115 m in depth and from a range of years (1954, 1970, 1971, 1973–1976). Values reported in Sell (1982) were converted to wet weight assuming 15% dry weight.

[b]Data from Lubner (1974, 1979).

[c]Data from Garner et al. (1988).

[d]Data from Sprules et al. (1991).

[e]Values represent range between production measured in nearshore (0–100 m) and offshore (>100 m) zones of Lake Ontario (see text for methods of calculation). Production estimated using bioenergetic model of Rudstam (1989).

[f]Values represent range between production measured at five different depth ranges (0–50, 50–100, 100–150, 150–200, and 200+ m). Production estimated using size-cohort analysis (described in Johannsson 1995). Values were converted to wet weight assuming 15% dry weight.

[g]Data from Johansson et al. (1985).

[h]Values represented range observed between sampling at a midlake station (CCIW station 41, the low value) and sampling at a station in the Kingston Basin (CCIW station 81) for the season April 1 to October 31.

[i]Production data for zooplankton expanded to the entire year based on methods described in text.

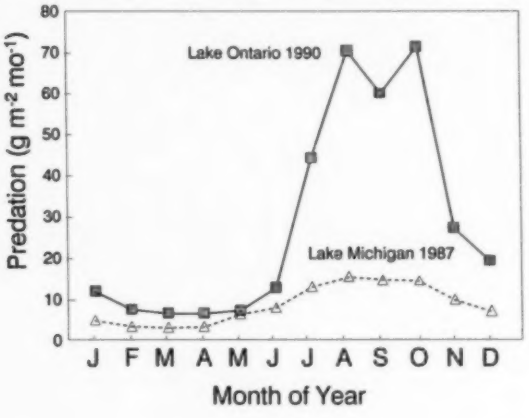
Effect of planktivore predation on available prey production

Zooplankton predation by planktivores in Lake Ontario exceeded prey production during 1990. The heaviest demand fell on copepods, with estimates of alewife predation exceeding available production by a factor of 2.7. Alewife demand on cladocerans was approximately equal to production in Lake Ontario (Fig. 7). The estimate of combined zooplankton predation (including alewife and rainbow smelt) was nearly double (1.6–1.7 times) that of production (Table 7). An early seasonal peak in zooplankton production (July) was followed by peaks in planktivory during August to October (Fig. 7). The general seasonal pattern indicates that predation exceeded available prey production in all months except July. Alewife larvae contributed markedly to total predation during July and August (Fig. 7).

Because no estimates of zooplankton production based on routine seasonal sampling were available for Lake Michigan in 1987, we compared an estimated range of production rates reported by Sprules et al. (1991) based on size-spectra theory with our estimates of zooplankton predation. The predation estimate (44.7 $g \cdot m^{-2} \cdot year^{-1}$) falls below the reported range of annual zooplankton production (72.1–91.6 $g \cdot m^{-2} \cdot year^{-1}$, Table 7). Planktivores were estimated to consume approximately 55% of the available zooplankton produced lake wide during 1987 (estimated by expanding mean value of 81.9 $g \cdot m^{-2} \cdot year^{-2}$ from Sprules et al. (1991) to the whole lake; Table 7).

Our estimates of *Mysis* predation by planktivores exceeded estimates of production in both lakes. The Lake Michigan planktivore predation rate on *Mysis* was greater than the range of production of *Mysis* reported by Sell (1982) for stations ranging in depth from 50 to 115 m. Lake-wide estimates of predation in Lake Michigan exceeded production by a factor of 1.3 (Table 7). The two estimates of annual production of *Mysis* in Lake Ontario differed by approximately 65% (205.1 $kt \cdot yr^{-1}$, using bioenergetic model; 337.9 $kt \cdot yr^{-1}$, using size-cohort analysis) and were both less than lake-wide estimates of planktivore predation on *Mysis* (Table 7).

Fig. 2. Total invertebrate predation (in units of wet grams per square metre per month) of the planktivore communities in Lakes Michigan (triangles) and Ontario (squares). Lake-wide predation was divided by respective lake surface areas to estimate areal predation.



Planktivores in Lake Michigan appear to be utilizing *Diporeia* to a greater degree than in Lake Ontario based on limited production values from studies during the 1980s (Table 7). Lake Michigan planktivores were estimated to consume over 100% of available annual production of the benthic amphipod, whereas planktivores in Lake Ontario consumed 75% of available *Diporeia* production.

Sensitivity analysis

The lake-wide consumption estimates for the larval and young-of-the-year age groups were generally the most sensitive to parameter perturbations (Table 8). The most sensitive parameters among those examined for both species models were lake-wide abundance and individual growth rates. The other parameters, in order of their sensitivity, were survival, temperature, and swimming speed. In only a few cases did a 10% change in parameter values propagate a deviation of ≥10% in estimated consumption rate by the populations. The alewife model was more sensitive than the bloater model to errors in values of water temperatures owing to the steepness of the respiration rate function at the higher water temperatures occupied by alewife during the summer growing season. Results of the sensitivity analysis of temperature on larval bloater consumption rates differed from that of alewife (Table 8). Because the occupied temperature for larval bloater set in the model approached their optimal feeding temperature (16.8°C; Rudstam et al. 1994), a 10% increase in occupied temperature placed the larvae in a suboptimal temperature regime, which translated into lower estimates of consumption compared with consumption rates estimated at the cooler water temperatures.

Discussion

The dynamics of production supply and demand allow us to make some generalizations about the pelagic predator–prey systems in Lakes Michigan and Ontario during 1987 and 1990, respectively. Planktivores consume much greater quantities of invertebrates and prey on smaller particle sizes in Lake Ontario than in Lake Michigan. This is due to the greater biomass per unit area of planktivores and the greater relative importance of microphagous alewife in Lake Ontario than in Lake Michigan. These conclusions are supported by independent observations of the zooplankton community in both lakes. Changes in the zooplankton community of Lake Ontario during the 1980s reflected strong top-down control by alewife (Johannsson et al. 1991; Johannsson and O'Gorman 1991; Mazumder et al. 1992); evidence of control was seen in both mean size and absolute abundance of zooplankters. Conversely, zooplankton in Lake Michigan are larger on average than in Lake Ontario (Sprules and Goyke 1994) and large-bodied zooplankton have increased in abundance since alewife became less dominant in the pelagia (Scavia et al. 1988; Evans 1990).

Our estimates of predation on microcrustacean zooplankton in Lake Ontario and *Mysis* in Lakes Michigan and Ontario exceeded our estimates of prey production. This imbalance has been noted in many river and stream studies (e.g., Allen 1951; Horton 1961; Mann 1965; Waters 1977) and has been termed "Allen's paradox" (Hynes 1970) after Allen (1951) who discovered this imbalance between brown trout and stream invertebrates in the Horokiwi

Fig. 3. Cumulative monthly predation (in wet weight) by the planktivore community in Lake Michigan by predator species (top panel) and prey type (bottom panel).

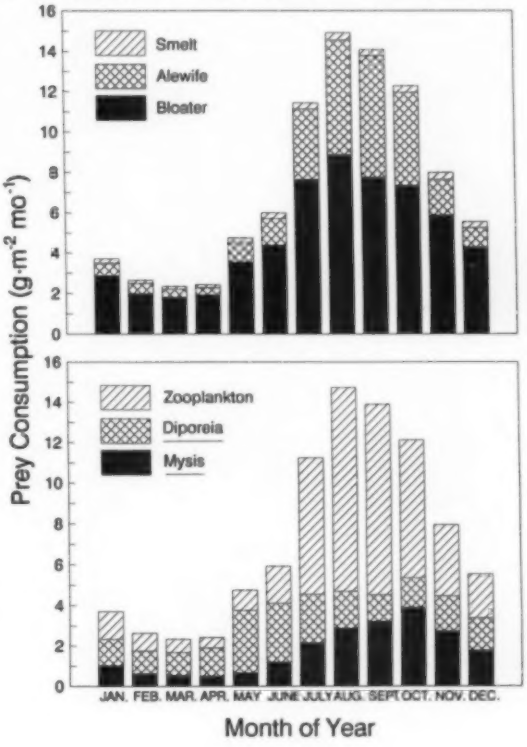


Fig. 4. Cumulative monthly predation by alewife in Lake Michigan by diet type (top panel) and age group (bottom panel).

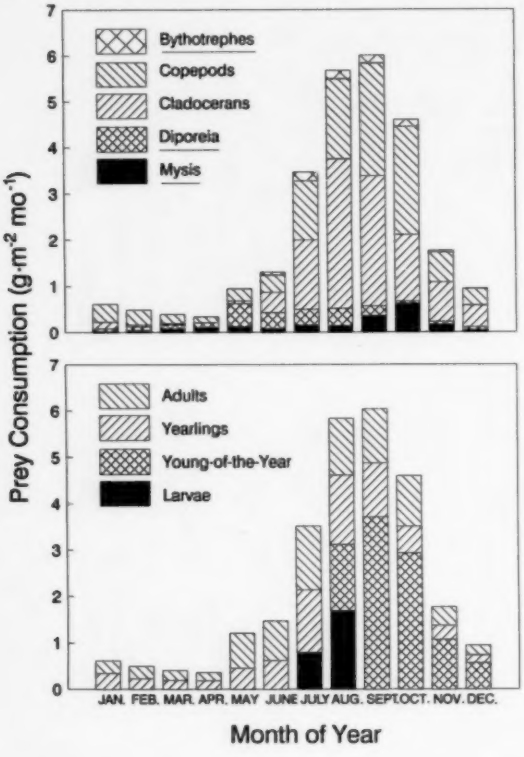
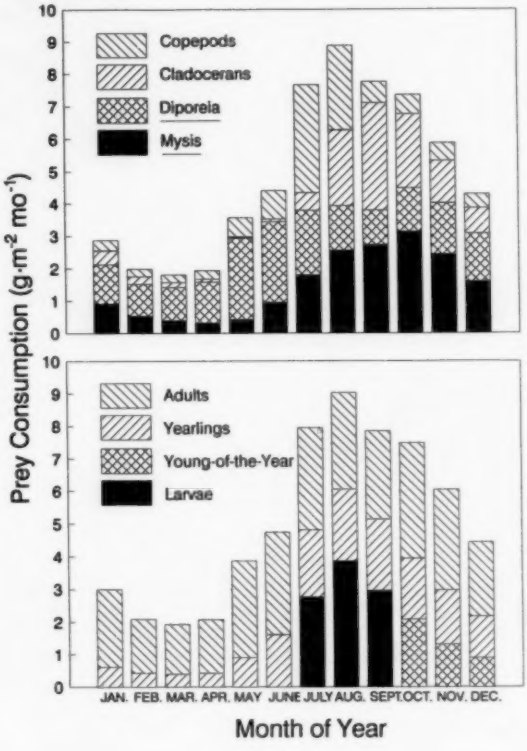


Fig. 5. Cumulative monthly predation by bloater in Lake Michigan by diet type (top panel) and age group (bottom panel).



stream in New Zealand. Investigators who have carried out these analyses in lakes, however, have arrived at different conclusions. The majority of recently published studies have found that planktivory by fish does not meet or exceed independent estimates of zooplankton production (e.g., Helminen et al. 1990; Luecke et al. 1990, 1992; Rudstam et al. 1992). In theory, if a predator–prey system is in trophic steady state, the processes of production and predation between adjacent trophic levels should balance. Zooplankton have relatively short generation times and very high turnover rates and, thus, cannot sustain levels of predation that exceed their intrinsic production rate.

The population of alewife in the Great Lakes have undergone major annual fluctuations in abundance (O'Gorman and Schneider 1986; Eck and Wells 1987; O'Gorman et al. 1987), and it has been hypothesized that this is a result of transitory periods of planktivore food limitation. It seems plausible that, under a scenario of several strong year-classes and favorable juvenile survival, planktivore demand for prey may approach levels of available prey production during a given period. Condition of individuals in the population would then decline and would become more susceptible to winter and spring die-offs (Bergstede and O'Gorman 1989), thus serving as a stabilizing ecosystem-level feedback. The decline in energy density in Lake Ontario alewife since the early 1980s (Rand et al. 1994) may have been a response to food limitation. The predator–prey imbalance noted in this modeling study indicates that food limitation may have been occurring during 1990 in Lake Ontario. More direct observations of alewife growth and condition during the fall of 1990 would have substantially reduced uncertainty in this study. Observations of lake-wide abundance of planktivores in Lake Ontario during 1991–1992 indicate that the population declined markedly from our abundance measures in 1990 (C. Schneider, NYSDEC, Cape Vincent, N.Y., personal communication), thus supporting our hypothesis that the rate of planktivore predation estimated during 1990 in Lake Ontario was not sustainable.

O'Gorman et al. (1991) demonstrated that alewife have the ability to locally deplete their zooplankton prey; hence, this trophic supply–demand imbalance could theoretically exist in some patches. However, our estimates of annual, lake-wide zooplankton predation by alewife in Lake Ontario integrated over the entire lake far exceeds that of zooplankton production (see Table 7), which points to some error in our approach or calculations. We carried out a great deal of spatial averaging in this study that may not be valid, especially for systems as large and spatially heterogeneous as the Great Lakes. There is a clear research need to measure and model predation and production processes on a finer spatial scale in the Great Lakes. This

Fig. 6. Cumulative monthly predation by alewife in Lake Ontario by diet type (top panel) and age group (bottom panel).

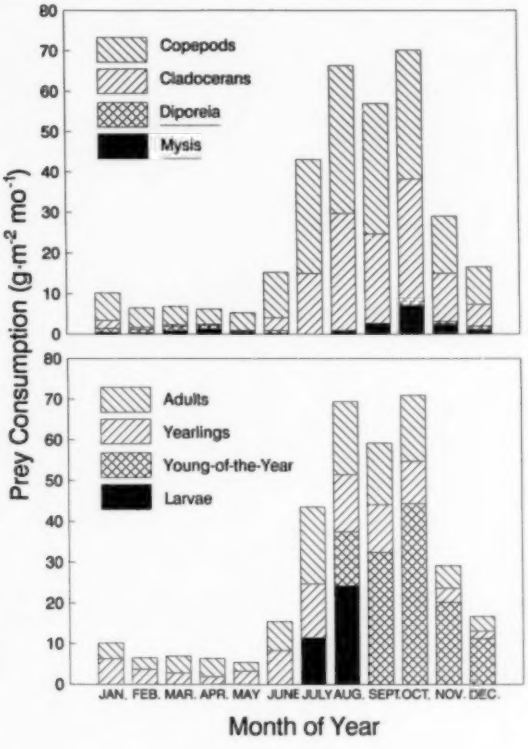
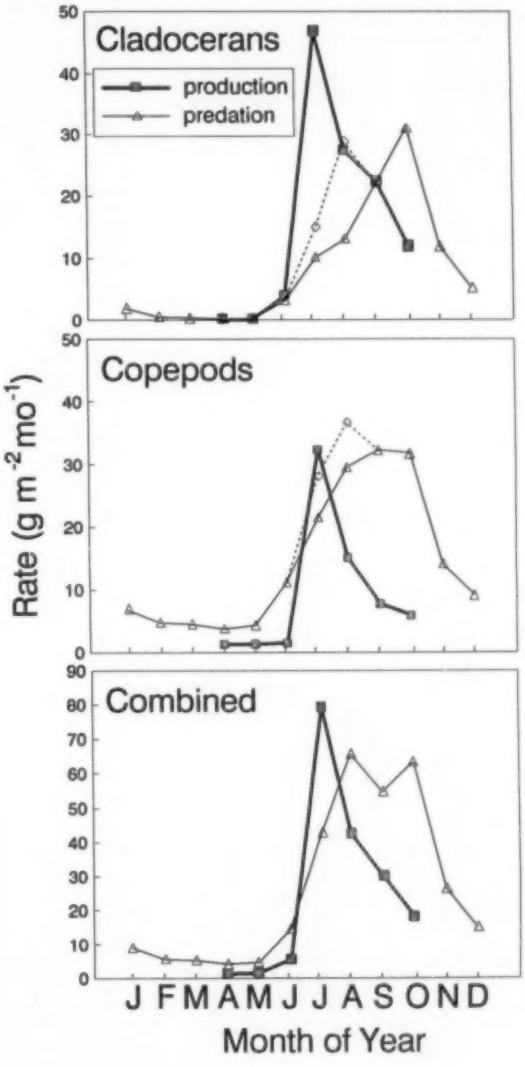


Fig. 7. Temporal sequence of zooplankton production and planktivore predation in Lake Ontario in 1990. The model results for consumption of cladocerans and copepods (top two panels) include only alewife predation because the available predation estimates for rainbow smelt did not partition the zooplankton prey into finer taxonomic categories. Broken lines in the top two plots represent predation including the contribution of alewife larvae. The bottom graph includes predation by both alewife and rainbow smelt.



approach requires spatial, synoptic sampling of both predators and prey. This sampling is now a real possibility given the recent advances in acoustics and optical plankton counting (e.g., Sprules and Goyke 1994).

The model estimates of zooplankton consumption in Lake Michigan appear to be more in line with levels of available production. The alewife population in Lake Michigan declined and remained relatively low during the middle and late 1980s, whereas bloater increased dramatically (Jude and Tesar 1985; Eck and Wells 1987). Epilimnetic zooplanktivory in Lake Michigan was relatively low during this period, and larger and more abundant zooplankton have been observed, which is consistent with food web theory (Kitchell and Crowder 1986; Scavia et al. 1988). The observed persistence of the large predatory cladoceran *Bythotrephes* in Lake Michigan (Sprules et al. 1990) supports the notion that rates of planktivory are low, at least relative to Lake Ontario. Further evidence of more favorable growth conditions in Lake Michigan is evident from higher estimates of energy density of alewife in Lake Michigan compared with Lake Ontario (Rand et al. 1994). Our results also support the hypothesis that planktivores (particularly bloater) are capable of controlling *Mysis* and *Diporeia* abundance in Lake Michigan, as espoused by McDonald et al. (1990). Although production estimates for these two invertebrate prey groups are limited, published values indicate that planktivore predation rates exceed available prey production during 1987. We relied on early estimates of *Mysis* production rates from Sell (1982). Lehman et al. (1990) reported densities of *Mysis* in Lake Michigan at a 100-m station that were similar to those used by Sell

Table 8. Summary of results of the parameter sensitivity analysis for the planktivore models.

		Proportional deviations from nominal run					
		Lake Michigan alewife		Lake Michigan bloater		Lake Ontario alewife	
Parameter	Age-class	+10%	−10%	+10%	−10%	+10%	−10%
Swimming speed	Larvae	0.05	−0.05	0.01	−0.01	0.05	−0.05
	YOY	0.02	−0.02	0.02	−0.02	0.03	−0.02
	Yearling	0.03	−0.03	0.02	−0.02	0.03	−0.03
	Adults	0.04	−0.03	0.03	−0.03	0.03	−0.03
	Combined	0.03	−0.03	0.02	−0.02	0.03	−0.03
Survival	Larvae	0.12	−0.11	0.14	−0.12	0.12	−0.11
	YOY	0.08	−0.07	0.01	−0.03	0.05	−0.04
	Yearling	0.03	−0.02	0.05	−0.07	0.03	−0.03
	Adults	0.01	−0.01	0.05	−0.08	0.01	−0.01
	Combined	0.05	−0.04	0.06	−0.08	0.04	−0.04
Temperature	Larvae	0.16	−0.11	−0.09	0.02	0.16	−0.11
	YOY	0.03	−0.03	0.04	−0.03	0.04	−0.04
	Yearling	0.07	−0.06	0.03	−0.02	0.05	−0.05
	Adults	0.05	−0.05	0.02	−0.01	0.04	−0.03
	Combined	0.06	−0.05	0.04	0.02	0.06	−0.05
Growth	Larvae	0.07	−0.08	0.10	−0.10	0.07	−0.11
	YOY	0.07	−0.07	0.08	−0.08	0.09	−0.04
	Yearling	0.10	−0.10	0.10	−0.10	0.09	−0.05
	Adults	0.13	−0.13	0.13	−0.04	0.12	−0.03
	Combined	0.10	−0.10	0.11	−0.07	0.10	−0.05

Note: Proportional deviations (±10%) from the nominal simulation are presented for Lake Ontario alewife and Lake Michigan alewife and bloater. Results are presented for each age-class seperately, and for all age-classes combined.

(1982) in his production calculations. Lehman et al. (1990) also reported densities of *Mysis* at a 150 m station that exceeded those used by Sell (1982), which indicates that we may have underestimated available *Mysis* production in the deep, offshore zone of Lake Michigan.

We cannot dismiss the possibility that our estimates are in error on both sides of the supply–demand comparison. Although our estimates of invertebrate production are the best available, there may be sources of error in sampling or data analysis. We extrapolated zooplankton production in Lake Ontario to the whole lake based on a mid-lake and a Kingston Basin station. A significant source of production could be occurring in the nearshore zones and embayments of the lake. Larvae typically occupy the warmer, more protected zones of the lake. We may have underestimated prey production available to them by not having zooplankton production data from these critical nursery areas. In addition, our estimates of microcrustacean zooplankton depended on some assumptions about hypolimnetic production and production rates over the unsampled winter period. Our current estimates may be underestimating available zooplankton production for foraging planktivores.

Our estimates of prey consumption using bioenergetic models may also be in error. In this paper we did not provide independent estimates of planktivore consumption. The process of model validation is necessary so that we can build confidence in bioenergetic models (Ney 1993). Predictions of the rainbow smelt model compared favorably with an empirical estimate of daily ration in Lake Michigan (Lantry and Stewart 1993). A study of herring (*Clupea harengus*) in the Baltic Sea indicated that a bioenergetics model predicted consumption rates twofold higher than empirical estimates (Arrhenius and Hansson 1994; S. Hansson, personal communication). The results of the latter study, in conjunction with the results of this study, may point to a consistent bias in estimates from bioenergetic models for clupeids. A yellow perch (*Perca flavescens*) bioenergetics model gave erroneous estimates of consumption in a number of lakes in Quebec (Boisclair and Leggett 1989). The authors suggest the reason for the disparity results from swimming speed variability that was estimated in the study by difference. The conclusions of the latter study have been criticized (Hayward 1990; Hewett et al. 1991) and subsequently defended by the authors (Boisclair and Leggett 1990, 1991). The reliability of this model remains in question. Our sensitivity analysis results indicate that a 10% error in predicted swimming speed would propagate errors in the range of 2–3% in the bloater and alewife models. Currently we have no in situ measures of the variability of swimming speeds for Great Lakes planktivores.

Possible variability in alewife swimming speed may be comparable with variability in swimming speeds of a related clupeid (Atlantic menhaden, *Brevoortia tryannus*). Durbin et al. (1981) measured volitional swimming speeds over

a fivefold increase in food density in laboratory tanks on 3-year-old menhaden (mean wet weight = 302 g, mean fork length = 25.8 cm) at 20 ± 1°C. The authors presented a hyperbolic function that described swimming speeds across the range of food densities. Swimming speeds increased sharply from nonfeeding periods over a gradient of food availability. Coefficients of variation of feeding individuals over 30 trials ranged from approximately 15 to 28% (mean was approximately 18%, from their Fig. 3). This variability in behavior applied to the modeled Great Lakes planktivores would translate into a potential error in consumption rates in the range of 5.6–8.4%. This error alone is not large enough to affect our conclusion that planktivory is higher in Lake Ontario than in Lake Michigan given the large discrepancy in the model estimated consumption rates. Nor is the error large enough to resolve the trophic supply–demand paradox. It does seem reasonable from observations made in the laboratory (Colby 1973; Stewart and Binkowski 1986) that alewife maintain a relatively high and consistent cruising speed during the day within tight schools, and variability may be lower than that estimated for yellow perch (Boisclair and Leggett 1989), YOY walleye (*Stizostedion vitreum*) (Madon and Culver 1993) and YOY brook trout (*Salvelinus fontinalis*) (Boisclair and Sirois 1993). The latter species are less adapted to a truly pelagic existence and their observed behaviors may not readily apply to fish like alewife, that generally inhabitant more pelagic habitats.

Our estimates of larval metabolism, a particularly sensitive parameter based on related studies (e.g., Hewett and Stewart 1989), may be in error. The common practice of back calculating larval metabolism using data measured on juveniles and adults may be inappropriate (e.g., Post 1990). There is a significant amount of scatter in the data on larval metabolism of clupeids (see Hewett and Stewart 1989, Fig. 3), and the model we used in this analysis may be overestimating respiration, which would lead to an overestimation of consumption rates. In fact, recent studies on rainbow smelt, yellow perch, and walleye suggest currently used parameters for larval metabolism (derived from juvenile and adult fish) tend to overpredict larval metabolism (B. Lantry, College of Environmental Science and Forestry, State University of New York, Syracuse, N.Y., unpublished data). If this is indeed the case for alewife, then appropriate changes to our model would result in lower estimates of predation by the YOY age-class.

One of the most sensitive parameters in these models was our estimates of the lake-wide population. A 10% change in abundance translates directly into a 10% deviation in model estimates of consumption. Additional field effort to quantify and reduce the uncertainty in lake-wide abundance should clearly be a priority. Our analysis also indicated the sensitivity of the parameters of the larval and YOY models. This has been observed in other studies (e.g., Hewett and Stewart 1989; Lantry and Stewart 1993). The survival and biomass estimates for the YOY and larval age-classes of alewife were among the most uncertain inputs in this modeling analysis and additional field work in this area is warranted.

The diet data used in our simulation for Lake Michigan alewife differed from those used by Hewett and Stewart (1989). Our diet data indicates alewife begin feeding on *Mysis* much earlier in their life history (spring yearlings) than suggested by Hewett and Stewart (1989). One of the possible explanations for this is that we have better sampling representation of alewife residing in an upwelling zone in Lake Michigan (particularly a sampled transect off Two Rivers, Wis.). This region of the lake is located near the intersection of the northern and southern basin gyres, which create an environment of upwelling. *Mysis* and *Diporeia* were found to be important diet items for rainbow smelt sampled in this region (Lantry 1991). In addition, more complete diel coverage of diet may have increased the relative importance of *Mysis* in the Lake Michigan diet data presented in this paper. Unfortunately, we did not have such a comprehensive data set on the diet of planktivores in Lake Ontario in 1990. In addition, the Lake Ontario diet data for the yearling and adult alewife collected during 1988 were from daytime bottom trawling samples, which may bias those diet composition estimates (Mills et al. 1992). Mills et al. (1992) also combined diet data for yearlings and adults, which may mask important dynamics in diet size selection by alewife, particularly for mysids.

Directions of future studies should include more comprehensive data on invertebrate biomass and production for Lake Michigan and better estimates of *Diporeia* and *Diacyclops* production in Lake Ontario. In addition, more work is needed to estimate rates of zooplankton production in nearshore regions and embayments in both lakes. Such data are especially important given rapidly expanding zebra mussel (*Dreissena* spp.) populations, which have the potential to drastically reduce phytoplankton densities in nearshore areas (Nicholls and Hopkins 1993). More detailed data on growth and survival of the larve and YOY of common planktivores, and how variable they are from year to year, would substantially improve our understanding of planktivory and, perhaps, help us determine which mechanisms are regulating fish recruitment.

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References

Allen, K.R. 1951. The Horokiwi stream: a study of a trout population. N.Z. Mar. Dep. Fish. Bull. 10: 238 p.

Arrhenius, F., and S. Hansson. 1994. In situ food consumption by young-of-the-year Baltic herring *Clupea harengus*: a test of predictions from a bioenergetics model. Mar. Ecol. Prog. Ser. 110: 145–149.

Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetic models. Can. J. Fish. Aquat. Sci. 43: 160–168.

Bergstede, R.A., and R. O'Gorman. 1989. Distribution of alewives in southeastern Lake Ontario in autumn and winter: a clue to winter mortalities. Trans. Am. Fish. Soc. 118: 687–692.

Boisclair, D., and W.C. Leggett. 1989. The importance of activity in bioenergetic models applied to actively foraging fishes. Can. J. Fish. Aquat. Sci. 46: 1859–1867.

Boisclair, D., and W.C. Leggett. 1990. On the relationship between growth and consumption rates: response to comments by R.S. Hayward. Can. J. Fish. Aquat. Sci. 47: 230–233.

Boisclair, D., and W.C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comment by Hewett et al. (1991). Can. J. Fish. Aquat. Sci. 48: 1337–1344.

Boisclair, D. and P. Sirois. 1993. Testing assumptions of fish bioenergetic models by direct estimation of growth, consumption, and activity rates. Trans. Am. Fish. Soc. 122: 784–796.

Brandt, S.B., D.M. Mason, E.V. Patrick, R.L. Argyle, L. Wells, P.A. Unger, and D.J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Can. J. Fish. Aquat. Sci. 48: 894–908.

Carpenter, S.R., [Ed]. 1988. Complex interactions in lake communities. Springer-Verlag, Berlin.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience, 35: 634–639.

Colby, P.J. 1973. Response of alewives, *Alosa pseudoharengus*, to environmental change, p. 163–198. *In* W. Chavin [ed.] Responses of fish to environmental changes. Charles C. Thomas, Springfield, Ill.

Crowder, L.B. 1986. Ecological and morphological shifts in Lake Michigan fishes: glimpses of the ghost of competition past. Environ. Biol. Fishes, 16: 147–157.

Crowder, L.B., and F.P. Binkowski. 1983. Foraging behaviors and the interaction of alewife, *Alosa pseudoharengus*, and bloater, *Coregonus hoyi*. Environ. Biol. Fishes, 8: 105–113.

Crowder, L.B., and H.L. Crawford. 1984. Ecological shifts in resource use by bloaters in Lake Michigan. Trans. Am. Fish. Soc. 113: 694–700.

Crowder, L.B., J.J. Magnuson, and S.B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Can. J. Fish. Aquat. Sci. 38: 662–668.

Durbin, A.G., E.G. Durbin, P.G. Verity, and T.J. Smayda. 1981. Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae). Fish. Bull. U.S. 78: 877–886.

Eck, G.W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of alewife (*Alosa pseudoharengus*). Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 53–60.

Evans, M.S. 1988. *Bythotrephes cederstroemi*: its new appearance in Lake Michigan. J. Great Lakes Res. 14: 234–240.

Evans, M.S. 1990. Large-lake responses to declines in the abundance of a major fish planktivore—the Lake Michigan example. Can. J. Fish. Aquat. Sci. 47: 1738–1754.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Am. Fish. Soc. 114: 328–337.

Gardner, W.S., T.F. Nalepa, W.A. Frez, E.A. Cichocki, and P.F. Landrum. 1985. Seasonal patterns of lipid content of Lake Michigan macroinvertebrates. Can. J. Fish. Aquat. Sci. 42: 1827–1832.

Goyke, A.P., and S.B. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Trans. Am. Fish. Soc. 123: 870–883.

Hayward, R.S. 1990. Comment on Boisclair and Leggett: can eating really stunt your growth? Can. J. Fish. Aquat. Sci. 47: 228–230.

Helminen, H., J. Sarvala, and A. Hirvonen. 1990. Growth and food consumption of vendance (*Coregonus albula* (L.)) in Lake Pyhajarvi, SW Finland: a bioenergetics modeling analysis. Hydrobiologia, 200/201: 511–522.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute, Madison, Wis. Tech. Rep. WIS-SG-92-250.

Hewett, S.W., C.E. Kraft, and B.L. Johnson. 1991. Consumption, growth, and allometry: a comment on Boisclair and Leggett (1989*a*, 1989*b*, 1989*c*, 1989*d*). Can. J. Fish. Aquat. Sci. 48: 1334–1337.

Hewett, S.W., and D.J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: Ontogenetic, seasonal and historical patterns. Trans. Am. Fish. Soc. 118: 581–596.

Horton, P.A. 1961. The bionomics of brown trout in a Dartmoor stream. J. Anim. Ecol. 30: 311–338.

Hynes, H.B.N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, U.K. 555 p.

Johannsson, O.E. 1985. Lake Ontario long term biological monitoring program report for 1981 and 1982. Can. Tech. Rep. Fish. Aquat. Sci. 1414: 208 p.

Johannsson, O.E. 1992. Life history and productivity of *Mysis relicta* in Lake Ontario. J. Great Lakes Res. 18: 154–168.

Johannsson, O.E. 1995. The response of *Mysis relicta* population dynamics and productivity to spatial and seasonal gradients in Lake Ontario. Can. J. Fish. Aquat. Sci. 52(7): 1509–1522.

Johannsson, O.E., E.L. Mills, and R. O'Gorman. 1991. Changes in the nearshore and offshore zooplankton communities in Lake Ontario: 1981–88. Can. J. Fish. Aquat. Sci. 48: 1546–1557.

Johannsson, O.E., and R. O'Gorman. 1991. Roles of predation, food, and temperature in structuring the epilimnetic zooplankton populations in Lake Ontario, 1981–86. Trans. Am. Fish. Soc. 120: 193–208.

Johannsson, O.E., L.G. Rudstam, and D. Lasenby. 1994. *Mysis relicta*: assessment of metalimnetic feeding and implications for competition with fish in Lakes Ontario and Michigan. Can. J. Fish. Aquat. Sci. 51: 2591–2602.

Jude, D.J., and F.J. Tesar. 1985. Recent changes in the inshore

forage fish of Lake Michigan. Can. J. Fish. Aquat. Sci. 42: 1154–1157.

Keilty, T.J. 1990. Evidence for alewife (*Alosa pseudoharengus*) predation on the European cladoceran *Bythotrephes cederstroemi* in northern Lake Michigan. J. Great Lakes Res. 16: 330–333.

Kitchell, J.F., and L.B. Crowder. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environ. Biol. Fishes, 16: 205–211.

Lantry, B.F. 1991. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. M.S. thesis, College of Environmental Science and Forestry, State University of New York, Syracuse, N.Y.

Lantry, B.F., and D.J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. Trans. Am. Fish. Soc. 122: 951–976.

Lehman, J.T., J.A. Bowers, R.W. Gensemer, G.J. Warren, and D.K. Branstrator. 1990. *Mysis relicta* in Lake Michigan: abundances and relationships with their potential prey, *Daphnia*. Can. J. Fish. Aquat. Sci. 47: 977–983.

Lubner, J.F. 1979. Population dynamics and production of the relict amphipod *Pontoporeia hoyi* at several Lake Michigan stations. Ph.D. thesis, University of Wisconsin, Milwaukee, Wis., 98 p.

Luecke, C., M.J. Vanni, J.J. Magnuson, J.F. Kitchell, and P.T. Jacobson. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: implications for the spring clear-water phase. Limnol. Oceanogr. 35: 1718–1733.

Luecke, C., L.G. Rudstam, and Y. Allen. 1992. Inter-annual patterns in planktivory 1987–1989: an analysis of vertebrate and invertebrate planktivores, p. 275–302. *In* J.F. Kitchell [ed.] Food web management: a case study of Lake Mendota. Springer Verlag, New York, N.Y.

Madon, S.P., and D.A. Culver. 1993. Bioenergetics model for larval and juvenile walleyes: an in situ approach with experimental ponds. Trans. Am. Fish. Soc. 122: 797–813.

Mann, K.H. 1965. Energy transformation by a population of fish in the River Thames. J. Anim. Ecol. 34: 253–275.

Mansfield, P.J., and D.J. Jude. 1986. Alewife (*Alosa pseudoharengus*) survival during the first growing season in southeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 1318–1326.

Mazumder, A., D.R.S. Lean, and W.D. Taylor. 1992. Dominance of small filter feeding zooplankton in the Lake Ontario foodweb. J. Great Lakes Res. 18: 456–466.

McDonald, M.E., L.B. Crowder, and S.B. Brandt. 1990. Changes in *Mysis* and *Pontoporeia* populations in southeastern Lake Michigan: a response to shifts in the fish community. Limnol. Oceanogr. 35: 220–227.

Mills, E.L., R. O'Gorman, J. DeGisi, R.F. Heberger, and R.A. House. 1992. Food of the alewife (*Alosa pseudoharengus*) in Lake Ontario before and after the establishment of *Bythotrephes cederstroemi*. Can. J. Fish. Aquat. Sci. 49: 2009–2019.

Nash, R.D.M., and A.J. Geffen. 1991. Spatial and temporal changes in the offshore larval fish assemblage in southeastern Lake Michigan. J. Great Lakes Res. 17: 25–32.

Nero, R.W., and W.G. Sprules. 1986. Zooplankton species abundance and biomass in relation to occurrence of *Mysis relicta* (Malacostraca: Mysidacea). Can. J. Fish. Aquat. Sci. 43: 420–434.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand–supply relationships between predators and prey. Rev. Aquat. Sci. 2: 55–81.

Ney, J.J. 1993. Bioenergetic modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122: 736–748.

Nicholls, K.H., and G.J. Hopkins. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and zebra mussel introduction. J. Great Lakes Res. 19: 637–647.

O'Gorman, R., R.A. Bergstedt, and T.H. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 390–403.

O'Gorman, R., E.L. Mills, and J.S. DeGisi. 1991. Use of zooplankton to assess the movement and distribution of alewife (*Alosa pseudoharengus*) in south-central Lake Ontario in spring. Can. J. Fish. Aquat. Sci. 48: 2250–2257.

O'Gorman, R., and C.P. Schneider. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Trans. Am. Fish. Soc. 115: 1–14.

Post, J.R. 1990. Metabolic allometry and larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. Can. J. Fish. Aquat. Sci. 47: 554–560.

Rand, P.S., B.F. Lantry, R. O'Gorman, R.W. Owens, and D.J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario: implications for salmonine energetics. Trans. Am. Fish. Soc. 123: 519–534.

Rice, J.A., L.B. Crowder, and M.E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. Trans. Am. Fish. Soc. 116: 703–718.

Rudstam, L.G. 1989. A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. J. Plankton Res. 11: 971–983.

Rudstam, L.G., F.P. Binkowski, and M.A. Miller. 1994. A bioenergetic model for analysis of food consumption patterns by bloater in Lake Michigan. Trans. Am. Fish. Soc. 122: 344–357.

Rudstam, L.G., S. Hansson, S. Johansson, and U. Larsson. 1992. Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar. Ecol. Prog. Ser. 80: 159–173.

Sell, D.W. 1982. Size–frequency estimates of secondary production by *Mysis relicta* in Lakes Michigan and Huron. Hydrobiologia, 93: 69–78.

Scavia, D., G.A. Lang, and J.F. Kitchell. 1988. Dynamics of Lake Michigan plankton: a model evaluation of nutrient loading, competition, and predation. Can. J. Fish. Aquat. Sci. 45: 165-177.

Sprules, W.G., S.B. Brandt, D.J. Stewart, M. Munawar, E.H. Jin, and J. Love. 1991. Biomass size spectrum of the Lake Michigan pelagic food web. Can. J. Fish. Aquat. Sci. 48: 105–115.

Sprules, W.G., and A.P. Goyke. 1994. Size-based structure and production in the pelagia of Lakes Ontario and Michigan. Can. J. Fish. Aquat. Sci. 51(11): 2603–2611.

Sprules, W.G., H.P. Riessen, and E.H. Jin. 1990. Dynamics of *Bythotrephes* invasion of the St. Lawrence Great Lakes. J. Great Lakes Res. 16: 346–351.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. 115: 643–661.

Urban, T.P., and S.B. Brandt. 1993. Food and habitat partitioning between young-of-year alewives and rainbow smelt in southeastern Lake Ontario. Environ. Biol. Fishes, 36: 369–372.

Warren, G.J., and J.T. Lehman. 1988. Young-of-the-year *Coregonus hoyi* in Lake Michigan: prey selection and influence on the zooplankton community. J. Great Lakes Res. 14: 420–426.

Waters, T.F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10: 91–164.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanogr. 15: 556–565.

Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates[1]

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Abstract: Lake trout (*Salvelinus namaycush*) growth rates were lower in Lake Superior (with the lowest prey density) than in Lakes Michigan and Ontario. In contrast, consumption rates (estimated using bioenergetics models) of lake trout were similar in Lakes Superior, Michigan, and Ontario because the primary prey in Lake Superior, rainbow smelt (*Osmerus mordax*), have a lower energy content than the primary prey in Lakes Michigan and Ontario, alewife (*Alosa pseudoharengus*). Estimated consumption rates did not respond to three- to five-fold changes in prey density within lakes and were similar across a 100-fold difference in prey density among lakes. These results demonstrate that lake trout are able to sustain high predation rates at low prey densities and a type II functional response fitted to these data rises very steeply at low prey densities. Two factors are implicated: the large search volume of these predators and disparity between the average density estimates of prey stock assessment and the spatial and temporal scaling appropriate for understanding predator–prey interactions. If prey are highly aggregated or predators can search large areas, then a decrease in whole-lake prey abundance will not necessarily result in a lower predation rate until prey populations are severely reduced.

Résumé : Le taux de croissance du touladi (*Salvelinus namaycush*) était plus bas dans le lac Supérieur (où la densité de proies était la plus faible) que dans les lacs Michigan et Ontario. Par contre, les taux de consommation (estimés à partir de modèles bioénergétiques) du touladi étaient similaires dans les trois lacs parce que la proie principale de l'espèce dans le lac Supérieur, l'éperlan arc-en-ciel (*Osmerus mordax*), a un contenu énergétique plus faible que sa proie principale dans les lacs Michigan et Ontario le gaspareau (*Alosa pseudoharengus*). Les taux de consommation estimés ne réagissaient pas à une multiplication par trois à cinq de la densité des proies à l'intérieur d'un même lac et étaient similaires dans les trois lacs même si la densité des proies était 100 fois plus élevée d'un lac à l'autre. Ces résultats révélent que le touladi peut maintenir un taux de prédation élevé lorsque la densité des proies est faible, et la réaction fonctionnelle de type II ajustée en fonction de ces données montre un accroissement très abrupt aux faibles densités de proies. Deux facteurs sont impliqués : d'une part, l'ampleur du volume d'eau dans lequel ces prédateurs recherchent la nourriture; d'autre part, la disparité entre les estimations de la densité moyenne dans l'évaluation du stock de proies et l'échelle spatio-temporelle permettant de comprendre les interactions entre les prédateurs et les proies. Si les proies sont fortement groupées ou si les prédateurs peuvent chercher leur nourriture dans une vaste zone, une baisse de l'abondance des proies dans l'ensemble du lac ne se traduit pas nécessairement par une baisse du taux de prédation, sauf si les populations de proies sont gravement réduites.

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Introduction

The Laurentian Great Lakes have a history of catastrophic change due to invasions by exotic species, overexploitation by fisheries, and disappearance of native stocks (e.g., Mills et al. 1993). Aggressive management actions have brought the invading sea lamprey (*Petromyzon marinus*) under control and have established piscivore populations through intensive stocking programs (Christie 1974). The result is greatly altered predator–prey systems. Large numbers of non-native salmonines are stocked including coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*). In combination with stocked populations of the native lake trout (*Salvelinus namaycush*), these predators now depend primarily on exotic forage species such as alewife (*Alosa pseudoharengus*) and smelt (*Osmerus mordax*) and to a much lesser degree on native species such as bloater (*Coregonus hoyi*) and lake herring (*Coregonus artedii*) (Stewart et al. 1981; Eck and Brown 1985; Brandt 1986; Negus 1992).

These altered systems currently support a recreational fishery estimated to provide $3–4 billion per year to local economies (Talhelm 1987). Because of strong public interest in the fishery and its immense economic benefits, there were strong incentives to increase hatchery capacity and stocking rates. For example, in Lake Ontario annual releases of all salmonines started at 76 000 fish in 1968, expanded to 2.8 million fish in 1974, to 4.5 million fish by 1980–1981, and to 8 million fish per year in 1984 (O'Gorman et al. 1987).

Increases in the stocking rates of lake trout, coho, and chinook in Lake Michigan raised concerns about the sustainability of the forage base. Stewart et al. (1981) predicted that populations of Lake Michigan's primary prey, the alewife, might decline or collapse if stocking rates were increased to intended levels of 15–16 million juvenile salmon per year. Those levels were reached in the early 1980s and the alewife population has since declined to less than 20% of former abundance (Kitchell and Crowder 1986; Kitchell 1991; Stewart and Ibarra 1991). Most recently, alewife populations in Lake Ontario have also declined (Jones et al. 1993) and fisheries managers have responded by reducing salmonid stocking rates.

Optimal stocking levels cannot be determined without knowledge of the lake's carrying capacity for these predators (Ney 1990). Knowing the historical response of stocked salmonines to changing prey resources provides one method for estimating a future, sustainable stocking level. Bioenergetics models and growth data have been used to estimate the magnitude of past predation (Stewart et al. 1981; Stewart and Ibarra 1991). This approach is useful, but limited. Predicting the results of the interactions between predators and prey populations requires an understanding of the feedback mechanisms between prey abundance, predation rates, prey choice, and the processes that affect predator growth and survival rates. Dynamic models of predator–prey interaction have been developed for several systems (Swartzman and Beauchamp 1990; Walters et al. 1980; Post and Rudstam 1992), including Lake Ontario (Jones et al. 1993).

In the analyses cited above, predation rates and predator growth rates are coupled to prey abundances through a functional response model (Holling 1959; Berryman 1992), which is used to estimate prey eaten per predator as prey populations change. These models are a central tenet of predator–prey theory presented in contemporary textbooks (Wootton 1990) and are a cornerstone of attempts to forecast effects of changes in salmonid stocking policy for the Great Lakes (Jones et al. 1993). This study was initiated with the goal of developing an empirical functional response model for lake trout in the Great Lakes.

Predation rates have been shown to vary with prey densities, but are also limited by water temperature and other physiological constraints. Estimates of the functional response of a predator can be derived from first principles of predatory search behaviors (Holling 1959), from laboratory experiments where prey density is varied and predation rates measured (e.g., Lyons 1987; Bergman 1987; Persson and Diehl 1990) or from field observations on consumption rates at different prey abundances (Swenson 1977). Predation rates can also be estimated through the use of bioenergetics models and compared with prey abundance (Rudstam 1989; Post 1990; Schneider 1992). Our analyses are based on the latter approach. The bioenergetics model applied here uses fish physiology, temperature, fish growth, diet composition, and caloric density of the predator and prey to estimate consumption by the predator (Hewett and Johnson 1992).

As a basis for developing this relationship, we analyzed empirical relationships between prey abundance, predator growth, and predation rates for populations of lake trout. In general, we expect growth to be dependent on prey abundance when the predator is food limited (e.g., Forney 1965). Specifically, we wanted to determine (1) how growth of lake trout responds to known changes in prey abundances and, therefore, (2) if predation rates (calculated from the bioenergetics model) can be predicted from prey abundances.

We based these analyses on Great Lakes lake trout populations because the lake trout is distributed throughout the lakes and, as the object of a consistent sampling effort by fishery agencies, provides a long-term record of age and growth data. We used prey abundance estimated from stock assessment trawl surveys conducted by the National Biological Survey (NBS, formerly U.S. Fish and Wildlife Service) in Lakes Michigan, Superior, and Ontario.

Methods

Information required to implement the bioenergetics models was derived from various sources as detailed in the following.

Growth rates, covering the period of 1978–1988, were calculated from average length at age data for Lake Michigan lake trout compiled by M. Miller (Wisconsin Department of Natural Resources (WDNR), Bureau of Water Resource Management 101 S. Webster St. Madison, WI 53707, personal communication) from annual, lakewide gillnet surveys conducted in fall. Although Lake Michigan creel survey data from 1969–1984 indicated that many salmon and trout creeled in Wisconsin waters did

Table 1. Length–weight regressions used in these analyses for Lakes Michigan and Superior. The slope and intercept values listed are the for the generalized equation: $\text{Log}_{10}(\text{weight}_{(kg)}) = b + a(\log_{10}(\text{standard length}_{(mm)}))$. Asterisks indicates length in millimetres total length and weight in grams. The Lake Ontario data was reported in both lengths and weights.

Lake and year	Slope (a)	Intercept (b)	Source
Lake Michigan			
1978–1979	3.12	−5.39*	Jensen et al. 1982
1980–1984	3.045	−7.92	Hagar 1985
1985	3.09	−8.22	M. Miller, personal communication
1986	3.21	−8.58	M. Miller, personal communication
1987	3.16	−8.44	M. Miller, personal communication
1988	3.24	−8.68	M. Miller, personal communication
Lake Superior			
1979–1984	3.266	−5.792*	Negus 1992

not decline in condition or weight during this period, lake trout had a greater mean weight, but a lower condition, than fish caught in 1937–1938 (Hansen 1986). Therefore, we calculated weights using length–weight regressions from Jensen et al. (1982) for 1978–1979, Hagar (1984) for 1980–1984, and M. Miller (address above, personal communication) for 1985–1988 (Table 1). Similarly, average length at age data for Lake Superior lake trout covered the period of 1978–1984 and were derived from Hansen's (1989) report describing annual, lake-wide spring assessment gillnetting of S. Schram (WDNR Box 589 Bayfield WI 54814, personal communication) and R. Schorfhaar (142 Aspen Drive, Marquette MI 49855, personal communication). The length-weight regression reported by Negus (1992) was used for Lake Superior fish (Table 1). Lake trout weight and length at age data of the annual lake-wide September gill net assessments of Lake Ontario from 1980–1985 were obtained from C. Schneider (NewYork State Department of Environmental Conservation, Box 165, Cape Vincent NY 13618, personal communication). Only growth data from known age, stocked lake trout were compared among lakes.

We analyzed data for two groups of similar-sized lake trout. The smaller size group was 43–56 cm in length. They represented age 4+ in Lake Michigan, age 6+ in Lake Superior, and age 3+ in Lake Ontario. The larger size group was 54–66 cm fish and were age 5+ in Lake Michigan, age 8+ in Lake Superior, and age 4+ in Lake Ontario. We chose these two separate size groups (versus age groups) to control for the effects of differential predation abilities and size specific vulnerability to the assessment gillnets or exploitation.

Diets of Lake Michigan lake trout were dominated by alewife and smelt. Other species, such as bloaters, may be included in the diet during fall and winter (Eck and Wells 1986; Stewart and Ibarra 1991; Fratt 1991). In Lake Superior, diets were dominated by smelt during 1978–1984 (Negus 1992). In Lake Ontario, lake trout consumed mainly alewife (75%) with smaller proportions of smelt (20%) and sculpin or other fishes (5%) (Christie et al. 1987; Brandt 1986). In the model, Lake Superior lake trout's diet consisted of 80% smelt, 10% coregonines, and 10% other fish. Between 1978 and 1988, the diet of lake trout in Lake Michigan shifted from mostly larger alewife to about 50% small alewife and other fish (Stewart and Ibarra 1991). This change was represented in the model. In 1978, the diet consisted of 65% large alewife, 15% small alewife, and 20% other fish. Beginning in the early 1980s, the percentage of small alewife and other fish (mostly smelt) increased and reached 20 and 30% of the lake trout diet by the mid-1980s.

For our comparison between consumption rates and prey abundance, we used assessment data for the primary prey populations, which were alewife and smelt in Lake Michigan, alewife in Lake Ontario, and smelt in Lake Superior. Whole lake biomass estimates of these prey species were obtained from areal expansions of trawl data for Lake Michigan from 1978 to 1988 (G. Eck, NBS, 1451 Green Road, Ann Arbor MI 48105, personal communication), for Lake Superior from 1978 to 1984 (Selgeby 1985), and for Lake Ontario from 1980 to 1985 (O'Gorman et al. 1987).

Predation rates were estimated using the lake trout bioenergetics model developed by Stewart et al. (1983) and the program package presented in Hewett and Johnson (1992). This model calculates the prey consumption necessary to account for the observed growth based on diet, prey and predator energy densities, and temperatures. Temperature regimes for Lake Michigan were taken from Stewart et al. (1983), for Lake Superior from Negus (1992), and for Lake Ontario from Rand et al. (1995). We assumed that lake trout will occupy the warmest available temperature up to but not exceeding the preferred temperature of 10°C. The hypolimnion of each lake reaches the preferred temperature for lake trout during early summer and cools to about 2–4°C during the late autumn. Differences in the temperature regimes for each lake are largely due to differences in the seasonal timing of warming and cooling.

Seasonal changes in alewife energy densities were obtained from Flath and Diana (1985) and Stewart and Binkowski (1986) for Lake Michigan and from Rand et al.

(1995) for Lake Ontario. Smelt energy densities were taken from Lantry and Stewart (1993) for Lakes Michigan, Superior, and Ontario. Energy density of lake trout was calculated as a function of fish weight (Stewart et al. 1983) and ranged between 2020 and 2470 $cal \cdot g^{-1}$ for the smaller fish and between 2170 and 2855 $cal \cdot g^{-1}$ for the larger fish.

The model was run for a 1-year time period. Since the timing of the growth estimates varied from lake to lake, the model was run for a year starting on the assessment date. Predator consumption rates were calculated as the overall average of weight specific consumption rates for the whole year. Parameters from a type II functional response model were estimated using the Quasi-Newton likelihood function in SYSTAT (Wilkinson 1990).

Results and discussion

Growth rates

Prey abundances within each lake varied approximately 10-, 5-, and 2-fold for Lakes Superior, Michigan, and Ontario, respectively. Growth rates of lake trout varied by a factor of two (Fig. 1). Annual growth rates were highest in Lakes Michigan (0.582–1.294 $kg \cdot yr^{-1}$) and Ontario (0.522–1.219 $kg \cdot yr^{-1}$), and lowest in Lake Superior (0.139–0.596 $kg \cdot yr^{-1}$), consistent with the differences observed in prey abundance. But, there was little effect of prey abundance on growth within lakes despite large differences in prey abundance among years (Fig. 1). Lakes Ontario, Michigan, and Superior had different lake trout diets, prey caloric content, and temperature. These factors could have contributed to the differences seen in growth rates among the lakes (see below).

Lake Superior lake trout growth increased slightly with prey abundance for both size classes, but correlations were low and the slopes of a linear regression were not statistically significant (small size class, $r^2 = 0.15$ and $p = 0.24$; large size class, $r^2 = 0.382$ and $p = 0.08$) (Fig. 1*a*). Lake Ontario lake trout showed decreasing growth when the prey density was over 100 kg·ha-1 (Fig. 1*c*). This trend was significant for the large size class ($r^2 = 0.802$, $p = 0.025$), but not for the smaller size class ($r^2 = 0.00$, $p = 0.4$). Lake Michigan lake trout growth was independent of prey density (small size class, $r^2 = 0.00$ and $p = 0.982$; large size class, $r^2 = 0.031$ and $p = 0.30$) (Fig. 1*b*).

Although fish growth rates are often correlated with prey abundance (e.g., Forney 1965), poor correlations between salmonid growth and estimates of prey abundance were noted by Hansen (1986) for lake trout in Lake Michigan, O'Gorman et al. (1987) for coho in Lake Ontario, and Brodeur (1992) for juvenile coho and chinook on the Oregon coast. The negative correlation between growth and prey abundance (Fig. 1) observed for Lake Ontario lake trout was also observed for Lake Ontario coho by O'Gorman et al. (1987). O'Gorman et al. (1987) hypothesized that decreased growth rates at high prey densities were due to poor condition of the prey. At high densities alewives have low lipid reserves and a lower caloric content, which may explain the negative correlation observed for lake trout.

This analysis demonstrated that growth rates are actually a poor indicator of prey abundance, which contradicts the arguments advanced by Kitchell and Crowder (1986). Prey populations are very difficult to sample effectively; therefore, we need an alternative early indicator of the condition of the forage base. A shift to smaller prey items in a highly size-selective predator, such as lake trout, may be such an indicator (Stewart and Ibarra 1991). In the early 1980s when alewife biomass declined in Lake Michigan, the proportion of large fish in the diet also declined (Stewart and Ibarra 1991). Hartman and Margraf (1992) also demonstrated an increase in the size range of prey for adult walleye when abundances of its primary prey declined.

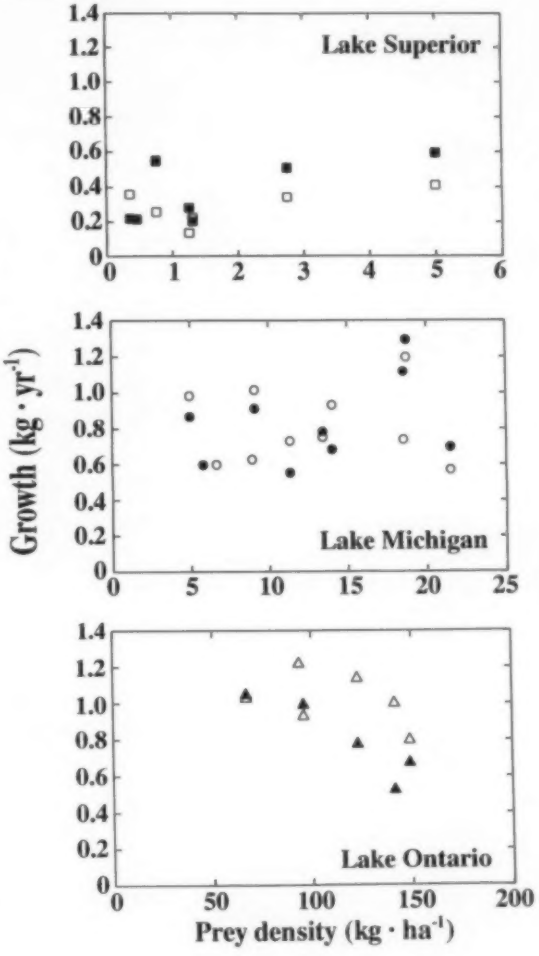
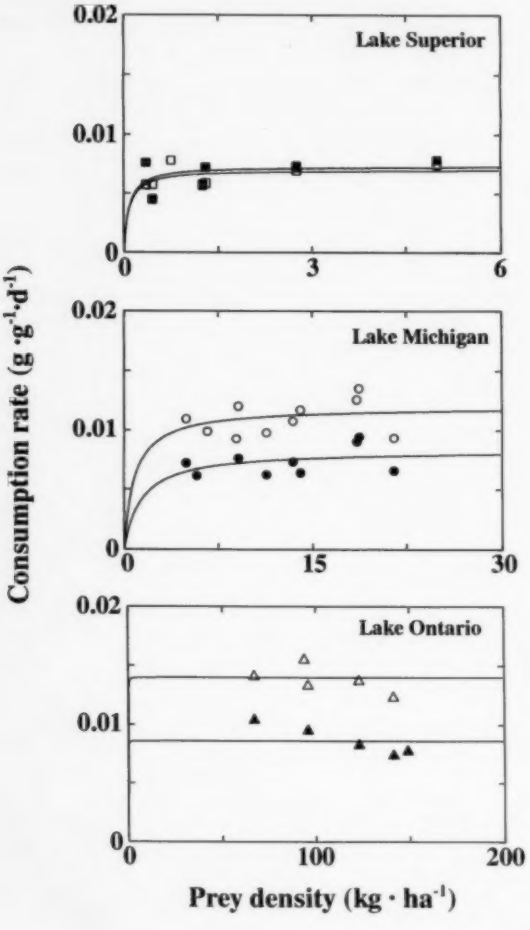


Fig. 1. Growth in kilograms per year for two size classes of lake trout as defined in the text. Open symbols represent the small size class and closed symbols represent the large size class. (A) Growth data for Lake Superior from 1978–1984 (Hansen 1989). (B) Growth data for Lake Michigan from 1978–1988 (M. Miller, personal communication). (C) Growth data for Lake Ontario from 1980–1985 (C. Schneider, personal communication).

Fig. 2. Consumption in grams per gram per day from the bioenergetics model for lake trout in each lake. Open symbols represent the small size class and closed symbols represent the large size class. (A) The type II functional response curves for Lake Superior are $y = (0.007N)/(0.075 + N)$ for the small size class, and $y = (0.007N)/(0.078 + N)$ for the large size class. (B) The equations for Lake Michigan data are $y = (0.012N)/(0.865 + N)$ for the small size class and $y = (0.008N)/(1.142 + N)$ for the large size class. (C) No equation is given for Lake Ontario because of the lack of the ability to define the curve well.



Although growth of lake trout showed no response to changing prey resources within each lake, growth of other more mobile predators, such as chinook or coho salmon, may be better indicators of prey abundance. There is evidence that both growth and mortality of chinook have responded to changes in prey density (Hansen 1986). Similarly, interannual differences in coho growth correspond with changes in prey abundance (Stewart and Ibarra 1991). Breck (1993) demonstrated that increases in the variance of growth rate may be the best indicator of declining prey abundance.

Consumption rates

Like growth rates, consumption rates derived from the bioenergetics model are weakly related to prey abundance (Fig. 2). In general, smaller fish have a higher specific consumption than larger fish, but larger fish have a greater total consumption. The differences between the average annual growth estimates within each lake are larger than differences in specific consumption estimates derived from the growth rates. Part of the reason for this is the high proportion of consumption (50–70%) that is used for maintenance in these fish.

But, consumption rates did not simply mirror interlake differences in growth rates. This is primarily because the energy content assumed for the prey differed among lakes. Although growth estimates of lake trout in Lake Michigan and Lake Ontario were similar, Lake Ontario lake trout consumed more prey because the energy density of alewife in Lake Ontario was lower than in Lake Michigan. Consumption rates of lake trout in Lake Superior and Lake Michigan were more similar than growth rates because Lake Superior lake trout fed on smelt which had a lower energy content than the alewife in Lake Michigan.

The type II functional response curves fit to the consumption estimates rise very steeply at low prey densities (Fig. 2). This was an unanticipated result given the growth rate responses during this time period for coho and chinook salmon (Stewart and Ibarra 1991). The curve suggests that, at low prey densities, a modest increase in prey resources may result in a large step change in predation rates.

There are several possible explanations for our results. Among the most important concern assumptions used in the analyses. First, the prey abundance as used in our analyses may not be a good measure of prey availability to lake trout. Some proportion of the prey fish biomass may include individuals larger than lake trout could consume. The size distribution of prey fish in predator's stomachs from Lake Michigan indicated that the largest alewives consumed by lake trout of the sizes we analyzed were approximately 200 mm (Miller and Holey 1992; Hagar 1984). Using available size and age distributions (Eck and Brown 1985), we excluded alewife larger than 200 mm from estimates of prey biomass. However, this had no effect on the relationships represented in Figs. 1 and 2.

The prey biomass estimates used in this study were derived from trawl catches made on an annual basis. Although these assessments are done with consistency and provide the best available indication of year to year differences, they do not reflect seasonal changes in prey biomass. Recent lakewide acoustic surveys indicate that the biomass of forage fish, particularly alewife and smelt, are greater than the estimates derived from the areal expansion of trawl data (Brandt et al. 1991). This discrepancy could help explain the observed high consumption rate at low prey abundances. Another possibility is that prey are spatially segregated from the lake trout, such as young-of-the-year prey occupying warmer temperatures than lake trout and, therefore, decreasing the available prey. The

data are annual prey biomass estimates based on spring or fall bottom trawl surveys and, as a result, do not account for the major seasonal changes in habitat partitioning. Habitat segregation would be most intense during summer stratification, thereby altering the biomass available to predators when energetic demands are high.

Diets used in these analyses may be biased because diets from Lakes Ontario and Michigan were compiled from angler-caught fish. On a lake-wide basis, adult lake trout may compensate for locally low alewife and smelt abundances by feeding on other prey, such as sculpin, to a larger degree than what is reflected in diets of angled fish. Diets from angled fish tend to have a higher proportion of alewife than those sampled through other methods (e.g., gill nets) (Hagar 1984; Miller and Holey 1992). Miller and Holey (1992) reported that diets of Lake Michigan lake trout taken in gillnet surveys were more diverse than those derived from angled fish. Angler orientation towards schools of prey fish may be the cause.

Given the large changes in prey abundances observed in recent years, we initially assumed that there would be comparable changes in predation rates and the degree of food limitation experienced by the lake trout. If confirmed by empirical evidence, a functional response link between predator and prey would allow monitoring of lake trout growth rates (low cost, high precision) to serve as a surrogate for monitoring of prey populations (high cost, low precision). Our analyses demonstrate that lake trout consumption rates did not respond over the 100-fold differences in prey abundance observed in the three lakes.

Reevaluation of assumptions made in developing functional response models may help determine if consumption rates are dependent on physiological restraints, such as search volume, rather than prey abundances. Holling's (1959) functional response equations are based on allocation of time by a predator and assumes that a predator is either searching for or handling prey; the latter includes time required for digestion. In a type II functional response, the number of prey consumed per predator per unit of time (C) is given by $C = vN/(1 + vNh)$ where N is prey abundance and h is the handling time. The prey encounter rate depends on the search volume and prey density. The search volume, v, depends on swimming speed of the predator, s, and the reactive distance, d. Therefore, $v = \pi d^2 s$.

To evaluate this effect, we used the parameters for swimming speed and reactive distance described in Jones et al. (1993). A swimming speed of one-half of a body length per second and a reactive distance of 40 cm was assumed for lake trout in Lake Ontario (Jones et al. 1993). Digestion rates of piscivorous brown trout have been estimated to be between 7–29% h^{-1} for different temperatures and prey sizes, taking between approximately 8–30 h to digest 90% of a meal (He and Wurtsbaugh 1993). Using the general temperature and prey size dependent exponential model from He and Wurtsbaugh (1993), a 50-cm lake trout consuming a 15-g prey item could have a handling time of 15 h. Assuming an average depth of 85 m for Lake Michigan, the half saturation levels (the prey density where one half of the maximum consumption rate occurs) is about 1.8 kg·ha^{-1} of prey. During the period used in our analyses, neither Lake Michigan nor Lake Ontario prey densities declined that low; therefore, lake trout may not be search limited in those lakes. Lake Superior prey densities did decline to below 1 kg·ha^{-1}, but the confidence intervals of trawl assessments are large.

Our half-saturation estimates for Lake Michigan are similar to the estimate used in the Lake Ontario model (Jones et al. 1993), but our calculated half saturation estimates for Lake Superior are lower. However, both estimates are considerably lower than those used in other dynamic models. For example, Madenjian and Carpenter (1991) used 116.9 mg·m^{-3} (14.5 kg·ha^{-1}, assuming an average depth of 12.4 m) for walleye in Lake Mendota, Post and Rudstam (1992) used 0.1331 g·m^{-3} (16.5 kg·ha^{-1}, assuming 12.4 m average depth) for piscivorous perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) in Lake Mendota, and Swartzman and Beauchamp (1990) calculated values of about 50 mg·m^{-3} (32.5 kg·ha^{-1}, assuming a 65-m average depth) for rainbow trout in Lake Washington.

Low half-saturation densities derived in our analyses may also be an artifact of spatial and temporal averaging. An underlying assumption of the functional response is that the prey are randomly distributed (Holling 1959). Therefore if prey densities decline, fewer prey are encountered and consumption decreases. If the prey are aggregated (e.g., in schools), a decrease in abundance will not result in a lower encounter rate until prey abundance is depressed to very low values. Also, the overlap in time and space of the predator and prey may vary among years and lakes. If spatially and temporally averaged data are not representative of density-dependent interactions in lakes, we must learn to explicitly describe the mechanisms that aggregate prey and predators as the appropriate basis for forecasting the outcome of predator–prey interactions. Spatially explicit data sets and high resolution predator–prey models, such as those developed by Brandt and Kirsch (1993), Goyke and Brandt (1993), and Mason and Patrick (1993), may provide the insights required to assess interactions between mobile predators and patchily distributed prey.

Nevertheless, at annual and whole-lake scales, our results suggest that lake trout will continue to feed at high and fairly constant levels across a wide range of prey abundances. This tends to destabilize models of predator–prey relationships because predators do not respond to higher prey abundances with increasing predation rates or to low prey abundances by decreasing predation. High predation rates at low prey abundances suggests that lake trout may exert a depensatory mortality on their prey when predation exceeds the productive capability of the prey. This occurred in the model by Jones et al. (1993) when the prey population fell into the "predator pit" as a result of variable overwinter mortality for alewife in Lake Ontario.

Our empirical analyses of lake trout consumption in these lakes support the modeling results of Jones et al. (1993). The predatory inertia built into long-lived predators like lake trout (Stewart et al. 1981) further complicates the apparent balance between predatory demand and prey supply in the Great Lakes and make these systems difficult to manage. Stocking policies set today translate into

predatory effects expressed several years from now. By extension, an undesirable decline in prey resources may represent decisions made several years before the evidence appears. Policy guidance based on observation will always be after the fact. Only a mix of mechanistic understanding and its expression in forecasting tools can offer guidance that prevents learning through disaster and (or) wasted opportunity.

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References

Bergman, E. 1987. Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. Environ. Biol. Fishes, 19: 45–53.

Berryman, A.A. 1992. The origins and evolution of predator–prey theory. Ecology 73: 1530–1535.

Brandt, S.B. 1986. Food of trout and salmon in Lake Ontario. J. Great Lakes Res. 12: 200–205.

Brandt, S.B., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Trans. Am. Fish. Soc. 122: 845–869.

Brandt, S.B., D.M. Mason, E.V. Patrick, R.L. Argyle, L. Wells, P.A. Unger, and D.J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Can. J. Fish. Aquat. Sci. 48: 894–908.

Breck, J.E. 1993. Foraging theory and piscivorous fish: are forage fish just big zooplankton? Trans. Am. Fish. Soc. 122: 902–911.

Brodeur, R.D. 1992. Factors related to variability in feeding intensity of juvenile coho salmon and chinook salmon. Trans. Am. Fish. Soc. 121: 104–114.

Christie, W.J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31: 827–854.

Christie, W.J., K.A. Scott, P.G. Sly, and R.H. Strus. 1987. Recent changes in the aquatic food web of eastern Lake Ontario. Can. J. Fish. Aquat. Sci. 44(Suppl 2): 37–52.

Eck, G.W., and E.H. Brown. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. 42: 449–454.

Eck, G.W., and L. Wells. 1986. Depth distribution, diet, and overwinter growth of lake trout (*Salvelinus namaycush*) in southeastern Lake Michigan sampled in December 1981 and March 1982. J. Great Lakes Res. 12: 263–269.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Am. Fish Soc. 114: 328–337.

Forney, J.L. 1965. Factors affecting growth and maturity in a walleye population. N.Y. Fish Game, 12: 217–232.

Fratt, T.W. 1991. Trophic ecology of burbot and lake trout in Green Bay and Lake Michigan with information for burbot on fecundity, gonadosomatic index, sea lamprey marks, and intestinal acanthocephalans. M.S. thesis, University of Wisconsin, Steven's Point, Wis.

Goyke, A.P., and S.B. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Trans. Am. Fish. Soc. 122: 870–883.

Hagar, J.M. 1984. Diets of Lake Michigan salmonids: an assessment of the dynamics of predator-prey interaction. M.S. thesis, University of Wisconsin, Madison, Wis.

Hansen, M.J. 1986. Size and condition of trout and salmon from the Wisconsin waters of Lake Michigan, 1969–84. Wis. Dep. Nat. Resour. Fish Manage. Rep. 126.

Hansen, M.J. 1989. Report to the Lake Superior committee, 1989 annual meeting, Lake Superior Technical Committee, March, Sault Ste. Marie, Ont.

Hartman, K.J., and F.J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Trans. Am. Fish. Soc. 121: 245–260.

He, E., and W.A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Trans. Am. Fish. Soc. 122: 717–730.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2: a generalized bioenergetics model for fish growth for microcomputers. Univ. Wis. Sea Grant Tech. Rep. WIS-SG-92-250.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Can. Entomol. 91: 385–398.

Jensen, A.L., S.A. Spigarelli, and M.M. Thommes. 1982. PCB uptake by five species of fish in Lake Michigan, Green Bay of Lake Michigan, and Cayuga Lake, New York. Can. J. Fish. Aquat. Sci. 39: 700–799.

Jones, M., J. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. Trans. Am. Fish. Soc. 122: 1002–1018.

Kitchell, J.F. 1991. Salmonid carrying capacity: estimates and experiences in the Great Lakes of North America. NOAA Tech. Rep. NMFS 102. pp. 59–66.

Kitchell, J.F., and L.B. Crowder. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environ. Biol. Fishes, 16: 205–211.

Lantry, B.F., and D.J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. Trans. Am. Fish. Soc. 122: 951–976.

Lyons, J. 1987. Prey choice among piscivorous juvenile walleyes (*Stizostedion vitreum*). Can. J. Fish. Aquat. Sci 44: 758–764.

Madenjian, C.P., and S.R. Carpenter. 1991. Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. Ecol. Appl. 1: 268–279.

Mason, D.M., and E.V. Patrick. 1993. A model for the space–time dependence of feeding for pelagic fish populations. Trans. Am. Fish. Soc. 122: 884–901.

Miller, M., and M. Holey. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. J. Great Lakes Res. 18: 51–60.

Mills, E.L., J.H. Leach, J.T. Carlton, and C.L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J. Great Lakes Res. 19: 1–54.

Negus, M.T. 1992. Evaluation of bioenergetics modeling in the study of predator–prey dynamics in Minnesota waters of Lake Superior. Minnesota Department of Natural Resources, Division of Fish and Wildlife, St. Paul, Minn. Invest. Rep. 414.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand–supply relationships between predator and prey. Rev. Aquat. Sci. 2: 55–81.

O'Gorman, R., R.A. Bergstedt, and T.H. Eckert. 1987. Prey fish dynamics and salmonine predator growth in Lake Ontario, 1978–84. Can. J. Fish. Aquat. Sci. 44: 390–403.

Persson, L., and S. Diehl. 1990. Mechanistic individual based approaches in the population/community ecology of fish. Ann. Zool. Fenn. 27: 165–182.

Post, J.R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. Can. J. Fish. Aquat. Sci. 47: 554–560.

Post, J.R., and L.G. Rudstam. 1992. Fisheries management and the interactive dynamics of walleye and perch populations, p. 381–406. *In* J.F.Kitchell [ed.] Foodweb management: a case study of Lake Mendota. Springer-Verlag, New York.

Rand, P.S., D.J. Stewart, B.F. Lantry, L.G. Rudstam, R. O'Gorman, G.W. Eck, A. Goyke, S.B. Brandt, and O.E. Johannsson. 1995. Effect of lake-wide planktivory by the fish community in Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. 52: 1546–1563.

Rudstam, L.G. 1989. A bioenergetics model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. J. Plankton Res. 11: 971–983.

Schneider, D.W. 1992. A bioenergetics model of zebra mussel, *Dreissena polymorpha*, growth in the Great Lakes. Can. J. Fish. Aquat. Sci. 49: 1406–1416.

Selgeby, J.H. 1985. Population trends of lake herring (*Coregonus artedii*) and rainbow smelt (*Osmerus mordax*) in U.S. waters of Lake Superior, 1968-84, p. 1-12. *In* R.L. Eshenroder [ed.] Presented papers from the Council of Lake Committees Plenary Session on Great Lakes Predator–Prey issues, March 20, 1985. Great Lakes Fish. Comm. Spec. Publ. 85-3.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. 115: 643–661.

Stewart, D.J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–1988. Can. J. Fish. Aquat. Sci. 48: 909–922.

Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fish and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

Stewart, D.J., D. Weininger, D.V. Rotters and T.A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40: 681–698.

Swartzman, G.L., and D.A. Beauchamp. 1990. Simulation of the effect of rainbow trout introduction in Lake Washington. Trans. Am. Fish. Soc. 119: 122–134.

Swenson, W. A. 1977. Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical environmental conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. J. Fish. Res. Board Can. 34: 1643–1654.

Talhelm, D.R. 1987. Economics of Great Lakes fisheries: an 1985 assessment. Special Economic Report of the Great Lakes Fishery Commission, Ann Arbor, Mich.

Walters, C.J., G. Steer, and G. Spangler. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey reduction. Can. J. Fish. Aquat. Sci. 37: 2133–2145.

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Ill.

Wootton, R.J. 1990. The ecology of teleost fishes. Chapman & Hall, London.

A spatially explicit bioenergetics measure of habitat quality for adult salmonines: Comparison between Lakes Michigan and Ontario[1]

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Abstract: We used spatially explicit modeling to compare habitat quality for chinook salmon, *Oncorhynchus tshawytscha*, and lake trout, *Salvelinus namaycush*, in Lakes Michigan and Ontario. This grid-based approach predicts a predator's physiological growth response, growth rate potential, from measured physical and biological environmental conditions and is a species-specific measure of habitat quality. Underwater acoustics was used to map prey spatial distributions, abundances, and sizes. A foraging model defined predator consumption rates from prey data. A bioenergetics model calculated growth rate potential based on consumption rates and prevailing thermal conditions. We compared habitat quality between lakes using both the mean growth rate potential and the volume (or proportion) of water capable of supporting positive growth rates. Mean growth rate potential for both chinook salmon and lake trout was similar between the lakes despite known differenes in the prey species composition and abundance. However, Lake Michigan provided a greater volume of water capable of supporting growth for both chinook salmon (26%) and lake trout (21%) compared with that for Lake Ontario (19% for both species). Our measure of habitat quality based on species-specific physiological requirements should provide a tool to compare ecosystems and quantify ecosystem change.

Résumé : Nous avons employé la modélisation spatialement explicite pour comparer la qualité de l'habitat du saumon quinnat (*Oncorhynchus tshawytscha*) et du touladi (*Salvelinus namaycush*) dans les lacs Michigan et Ontario. Cette approche par quadrillage permet de prédire la réaction du prédateur sur le plan de la croissance physiologique ainsi que son taux de croissance potentiel, à partir de mesures des conditions physiques et biologiques de l'environnement, et d'obtenir pour chaque espèce une mesure de la qualité de l'habitat. Des méthodes acoustiques nous ont permis de cartographier la répartition spatiale, l'abondance et la taille des proies. Un modèle de la recherche de nourriture nous a permis d'établir le taux de consommation des prédateurs à partir des données sur les proies. Un modèle bioénergétique nous a enfin permis de calculer le taux de croissance potentiel à partir des taux de consommation et des conditions thermiques qui prévalaient. Nous avons comparé la qualité de l'habitat des deux lacs en nous servant à la fois du taux de croissance potentiel moyen et du volume (ou de la proportion) de l'eau autorisant des taux de croissance positifs. Les taux de croissance potentiels moyens du saumon quinnat et du touladi étaient à peu près les mêmes pour les deux lacs, malgré les différences connues dans la composition spécifique et l'abondance des proies. Toutefois, le lac Michigan offrait un plus grand volume d'eau pouvant favoriser (26% pour le saumon quinnat et 21% pour le touladi) que le lac Ontario (19% pour les deux espèces). Notre mesure de la qualité de l'habitat fondée sur les exigences physiologiques de chaque espèce devrait permettre de comparer les écosystèmes et de quantifier les modifications qu'ils subissent.

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Introduction

Salmonines in Lakes Michigan and Ontario are showing signs of stress that may have serious repercussions on the existing multibillion dollar sports fishery (Talhelm 1988). In Lake Michigan, salmonines have apparently experienced decreased growth rates and a decrease in hatchery returns suggesting reduced habitat quality and increased mortality rates of salmonines (Stewart and Ibarra 1991). In Lake Ontario, reduced growth rates and reduced maturation rates of coho salmon, *Oncorhynchus kisutch*, have been associated with poor year classes of alewife, *Alosa pseudoharengus*, and recently an unusually high number of dead salmon were recovered in bottom trawls (Jones et al. 1992).

Lack of quantitative data on the capacity of Lakes Michigan and Ontario to support salmonine growth and production has resulted in controversy over the appropriate stocking rates of salmonines (Keller et al. 1989; Hansen et al. 1990). Alewife, the primary prey of stocked salmonines (Hagar 1984; Jude et al. 1987; Brandt 1986; McComish 1989; Stewart and Ibarra 1991), have declined in abundance in both lakes (Jude and Tesar 1985; Eck and Wells 1987; Evans 1990; Jones et al. 1992). Recent declines in the condition of stocked salmonines in Lake Michigan has been associated with the decline in alewife abundance (Stewart and Ibarra 1991). However, despite the decline in alewife abundance, total prey fish biomass (alewife, bloater, *Coregonus hoyi*, and rainbow smelt, *Osmerus mordax*) is the highest in recorded history (Rudstam et al. 1994).

The quality of a habitat is best considered in terms of the physical (e.g., temperature, dissolved oxygen concentrations, light intensity, and turbidity) and biological characteristics (e.g., prey fish abundance and size structure) of the environment. For example, optimal temperature for individual fish growth is of little value for defining the quality of the environment if prey species are unavailable either through spatial segregation or an unsuitable size distribution. The heterogenous nature of the physical environment and the complex spatial arrangement of predator and prey in space and time must be considered (e.g., Brandt et al. 1992). Recent applications of spatially explicit modeling in aquatic systems have included an analysis of the spatial patterns of planktivory (Luo and Brandt 1993), quantifying the seasonal growth potential of striped bass (*Morone saxatilis*) in the Chesapeake Bay (Brandt and Kirsch 1993), and quantifying the seasonal importance of spatial location of salmon and their prey along thermal gradients in Lake Ontario (Goyke and Brandt 1993).

Our objectives were to (1) introduce an application of the spatially explicit models of Brandt et al. (1992) to functionally define and quantify habitat quality with respect to the physiological needs of targeted fish species, (2) compare the habitat quality of Lake Michigan and west-central Lake Ontario for two species, a 5-kg chinook salmon and a 4-kg lake trout, and (3) provide an evaluation of the general approach. We selected chinook salmon and lake trout predators because chinook salmon account for the majority of fish stocked in Lakes Michigan and Ontario (Hansen et al. 1990; LeTendre and Savoie 1992), chinook have dominated the recreational catch (Hansen et al. 1990), and chinook consume the greatest proportion of alewife production compared with the other stocked salmonines (Stewart et al. 1981; Brandt et al. 1991). Lake trout have historically been the dominant top predator, were an important component of the commercial catch, are intensively stocked in an effort to reestablish a self sustaining population (Elrod 1983), and are considered an indicator species for environmental quality (Edwards et al. 1990; Ryder 1990). In addition, chinook salmon and lake trout represent an interesting ecological contrast with different physiology and different temperature preferences (Stewart and Ibarra 1991).

General approach and model

Defining the quality of an ecosystem requires social, economic, and biological information (Costanza et al. 1992). We simplify this idea and define habitat quality only in terms of the physical and biological conditions of the habitat and the physiology of the predator (i.e., quality is defined on a species by species basis). We adapt the "scope for growth" concept for operationally defining habitat quality as applied to individual species (Costanza 1992). Scope for growth is defined as the difference between energy available for maintenance and energy available for all other purposes (e.g., somatic growth, reproduction, activity).

Individual growth rate potential can be used as an indicator of habitat quality. Growth rate potential is the expected growth rate of a predator if placed in a particular volume of water with known biological (food resources) and physical (temperature) characteristics, independent of actual predator distribution and actual growth rates. Thus, growth rate potential reflects the individual's response to environmental conditions, overall activity level, and metabolic requirements. As such, growth rate directly reflects habitat quality, i.e., species-specific growth rates provide an index of habitat quality with maximum growth rate reflecting the highest quality habitat. High growth rates in fish are believed to improve survivorship, may be responsible for good year-classes, and allow individuals to reach a larger size at age (Houde 1987; Pepin and Myers 1991). Furthermore, the largest females in a population often produce larger and more viable eggs that may enhance larval survival (Zastrow et al. 1989; Monteleone and Houde 1990). Thus, growth rate is an indicator of an individuals well being and provides a link between individuals, population, and evolutionary fitness.

In large pelagic ecosystems, prey fish distributions are often spatially patchy and the physical environment also varies across space and time. How can the spatial complexity of the biological and physical components of an ecosystem be integrated into a single measure of habitat quality? We apply a grid-based approach to incorporate spatial complexities. Columns in the grid represent horizontal distance (e.g., running from inshore to offshore) and rows represent depth from surface to bottom. Each cell (defined on a volume) has a measured prey fish density, prey fish size, and water temperature. The spatial grid is defined by the spatial distribution of the food resource as well as the heterogeneous thermal environment. A foraging

Fig. 1. Location of sampling transects in Lake Michigan (left) and Lake Ontario (right). Note the length of the transects are not to scale.

model and a physiological growth model are then run in each cell to calculate growth rate potential of a fish if placed in that particular cell. Inputs into the foraging model include prey density and prey size with consumption rate as the output. The physiological growth model uses consumption rate from the foraging model and temperature as inputs and predicts (estimates) growth rate potential. For further details see Brandt et al. (1992). To implement this approach, spatial data on the biological and physical conditions of the environment are needed, specifically, prey density, prey size, and water temperature.

Methods

Field sampling

Acoustics can be used to continuously measure the spatial distribution and size structure of pelagic organisms (A. Goyke, S.B. Brandt, and D.M. Mason, unpublished data[3]). The acoustics provides the spatial template for the model grid. Summer data from Lake Michigan (26 August to 10 September 1987) and west-central Lake Ontario (30 July to 3 August 1990) were used for our modeling application. Acoustic data were collected continuously along transects that were run from nearshore to offshore to a maximum water depth of 110 m at five locations for Lake Michigan and from nearshore to beyond the 110-m bathymetric contour for three locations in west-central Lake Ontario (Fig. 1). Sampling commenced about 1 h after dark and ceased just before dawn. Acoustic transducers were housed in a stable platform and towed alongside the ship at speeds of about 3.0 $m \cdot s^{-1}$ for Lake Michigan and 2.5 $m \cdot s^{-1}$ for Lake Ontario. Temperature was recorded surface to bottom using a mechanical bathythermograph for Lake Michigan and an electronic bathythermograph for Lake Ontario at fixed locations along the transects. Bottom trawls and midwater trawls were used to identify acoustic echoes to species (Brandt et al. 1991; A. Goyke, unpublished data). Detailed descriptions of the acoustics and the sampling programs, which can be found in Brandt et al. (1991) for Lake Michigan and Goyke and Brandt (1993) for Lake Ontario, are only briefly summarized below.

A 120 kHz dual beam (10°, 25°) echo sounder (Biosonics model 102) was used to measure the spatial distribution, density and size of pelagic prey fishes (Table 1). Equipment performance was monitored in the field using a chart recorder and an oscilloscope. Signals were adjusted using a 40 $\log_{10}$ R (where R is range from transducer) time varied gain (TVG), digitized, and recorded on VHS video cassette tapes for later analyses in the laboratory. Reference voltages were recorded on each video cassette tape to calibrate signals before analysis. Overall system performance of the acoustic equipment was determined during each survey using a tungsten carbide reference sphere of known target strength (Foote et al. 1987; Foote 1990).

Acoustic data were processed using both echo-squared integration and dual-beam analyses. Echo-squared integration provides a measure of relative fish density that can be scaled to absolute fish density using system parameters obtained from equipment calibration and the mean backscattering coefficient obtained from dual-beam analysis. Echo-squared integration (Powell and Stanton 1983; Thorne 1983) was done on the narrow (10°) beam using an echo integrator (Biosonics model 221). For both lakes, the water column was divided into 100 one-meter vertical strata beginning 2.5 m from the transducer. The echo integrator averaged echo returns at 25-s (Lake Michigan) and 30-s (Lake Ontario) intervals corresponding to a horizontal resolution of about 75 m at a boat speed of 3.0 $m \cdot s^{-1}$ (Lake Michigan) and 2.5 $m \cdot s^{-1}$ (Lake Ontario). Echo-squared integration values were corrected for signal spreading by adjusting the 40 $\log_{10}$ R TVG to a 20 $\log_{10}$ R TVG in our software before applying the mean backscattering coefficient (see below).

Dual-beam analyses (Traynor and Ehrenberg 1979; Burczynski and Johnson 1986) was done using a dual-beam processor (Biosonics model 281) to determine the depth distribution of fish backscattering coefficients ($\overline{\sigma_{bs}}$) and fish target strength (TS). Only single targets from 0 to 3.0° off-axis were used in the analyses (Burczynski and Johnson 1986; Burczynski et al. 1987). Mean backscattering coefficients were calculated for each cell (75 m horizontal and 1 m vertical) to convert echo-squared integration into measures of absolute fish density. Target strength values at depth were converted to estimates of fish length using an empirical relationship developed by Love (1977). Love's (1977) equation adequately describes the fish length versus fish target strength relationship of Great Lakes pelagic fishes (Brandt et al. 1991).

The models

Models were run on a grid defined by the horizontal and vertical extent of the acoustic data, i.e., the horizontal

[3] Goyke, A., S.B. Brandt, and D.M. Mason. Distribution, abundance, and size structure of pelagic planktivores in Lakes Michigan and Ontario. Unpublished MS.

Table 1. System parameters and equipment calibration for acoustics.

Lake	Source level (dB re μPa @ 1 m)	Overall system gain (dB re μPa @ 1 m)		Transducer beam pattern b_{av}^2 (θ)	Pulse width (ms)	Sampling rate (pings·min^{-1})
		20 $\log_{10}$ R	40 $\log_{10}$ R			
Michigan	215.4	−172.48	−173.98	0.002 928	0.5	48
Ontario	219.4	−142.2	−159.9	0.002 308	0.5	40

distance traversed along the transect and the maximum depth of the transect. Acoustic data were standardized so that the end of the transects occurred at a bottom depth of about 100 m for both lakes. The horizontal extent of each transect ranged from a minimum of 7.9 km (Frankfort, Mich.) to a maximum of 21.2 km (Waukegan, Ill.). Individual cell size was determined by the sampling resolution of the acoustics (75 m horizontal, 1 m vertical). Water temperatures at depth between sampling stations were determined by linear interpolation. Thus, each cell contained a value for average prey fish density, average prey fish size, and average water temperature. These data were used as inputs to foraging and growth models. A foraging model and a physiological growth model were then run for each cell within the grid, independent of the actual distribution of the chinook salmon and lake trout, to provide a local growth rate potential.

Several foraging models could be used for this application. We considered foraging rate to consist of a series of chronological events, an encounter rate (E) and a combination of probabilities including detection (recognition), attack, capture, and ingestion of prey. We combined the probabilities into one term, P, and defined feeding rate (number of prey eaten per predator per unit time), ϕ, as

$$[1] \quad \phi = EP$$

To simplify this expression, we assumed that $P = 1.0$ because little is known of the values for the sequence of probabilities for salmonines. The implication of this assumption is that foraging rate will be maximized (D.M. Mason and S.B. Brandt, personal observation).

Predator encounter rate with prey (number per unit time) was assumed to be a function of the reactive distance of predator j to prey i (R_{ij}), prey swimming speed (v_i), predator swimming speed (v_j), and prey density (u_i). We used the encounter rate model developed by Gerritsen and Strickler (1977):

$$[2] \quad E = \frac{\pi R_{ij}^2}{3}\left(\frac{3v_j^2 + v_i^2}{v_j}\right)u_i, \qquad \text{for } v_i \le v_j$$

We assumed that a salmonine predator could detect a prey fish at 0.5 m ($R_{ij} = 0.5$) (Goyke and Brandt 1993). Swimming speed for pelagic prey fish was 0.2 m·s^{-1} (Rudstam et al. 1984; Stewart and Binkowski 1986). Predator swimming speed (metres per second) was assumed to be a function of weight and temperature (T). For a 5-kg chinook salmon (see below), $v_j = 0.289e^{0.0405T}$ (Beauchamp et al. 1989; Stewart and Ibara 1991) and for a 4-kg lake trout (see below) $v_j = 0.180e^{0.0405T}$ (Stewart et al. 1983).

Chinook salmon and lake trout were then assumed to forage throughout the night when estimates of the pelagic distribution and abundance of prey fish were available. Number of prey fish consumed was converted to biomass consumed based on a composite length–weight relationship developed from alewife, bloater, and smelt for Lake Michigan and alewife and smelt for Lake Ontario. Length (L; millimetres) was converted to weight (W; grams) using the relationship $W = 1.17 \times 10^{-6}L^{3.359}$ for Lake Michigan (Brandt et al. 1991) and $W = 1.94 \times 10^{-6}L^{3.238}$ for Lake Ontario (Goyke and Brandt 1993). Length of prey consumed was assumed to be the mean length of prey fish found in an individual cell.

We modeled the growth rate potential (weight per unit time) of a 5-kg chinook salmon and a 4-kg lake trout using the bioenergetics model of fish growth (Hewett and Johnson 1987, 1992). The bioenergetic model is a species-specific, energy-balance approach that describes the flow of energy through an individual fish and how that energy is partitioned among consumption, growth (somatic and reproductive), and losses (respiration, egestion, excretion, and specific dynamic action). Energy per unit time is related to weight per unit time by a specific energy density for predator and prey (calories per unit weight). The basic form of the bioenergetics model in terms of weight-specific growth rate (grams per gram per day) is

$$[3] \quad \frac{1}{W}\frac{dW}{dt} = \phi - (R_{resp} + SDA + F + U)$$

where W is weight of the individual predator, t is time in days, ϕ is predator feeding rate, R_{resp} is respiration, SDA is specific dynamic action, F is egestion, and U is excretion.

Predator feeding rate ϕ is an input to the model; however, daily feeding rate is constrained by temperature and weight dependent maximum consumption. That is, an individual fish cannot consume more than it can contain, assimilate, and evacuate in a single day. Feeding rate is thus bounded by a maximum consumption function. Species-specific maximum consumption, ϕ_{max}, is described by the equation:

$$[4] \quad \phi_{max} = aW^b f(T)$$

where a and b are the parameters of the weight dependence of consumption, and $f(T)$ is the species-specific temperature-dependent function of consumption (Hewett and Johnson 1992). Thus, consumption rate, as determined by the foraging model, cannot exceed ϕ_{max}. The equations describing the other components of the bioenergetics model (R_{resp}, SDA, F, and U) and the values for the physiological

Table 2. Mean prey fish density ($g \cdot m^{-3}$), with range given in parentheses, for distinct regions in the water column for all transects in Lake Michigan and Lake Ontario.

Location	Hypolimnion ($3.9 \leq T \leq 10°C$)	Metalimnion ($10 < T < 16°C$)	Epilimnion ($T \geq 16°C$)	Overall (SE)[a]
Lake Michigan				
Frankfort	0.022 (0–3.9)	0.121 (0–2.1)	0.207 (0–15.5)	0.052 (0.070)
Ludington	0.013 (0–0.8)	0.055 (0–1.8)	0.235 (0–24.7)	0.075 (0.071)
Sturgeon Bay	0.008 (0–0.6)	0.005 (0–1.2)	0.072 (0–22.1)	0.029 (0.013)
Two Rivers	0.012 (0–2.3)	0.037 (0–2.8)	0.649 (0–46.4)	0.156 (0.215)
Waukegan	0.019 (0–12.9)	0.066 (0–2.0)	1.147 (0–194.3)	0.250 (0.386)
Mean (SE)	0.015 (0.003)	0.057 (0.019)	0.462 (0.197)	0.133 (0.042)
Lake Ontario				
Toronto	0.001 (0–0.2)	0.056 (0–11.8)	0.269 (0–49.4)	0.055 (0.090)
Port Weller	0.002 (0–1.0)	0.353 (0–42.8)	0.977 (0–156.7)	0.130 (0.361)
Cobourg	0.001 (0–0.3)	0.005 (0–0.6)	1.237 (0–213.9)	0.259 (0.426)
Mean (SE)	0.001 (<0.001)	0.138 (0.109)	0.828 (0.289)	0.142 (0.060)

[a]Overall column and row means are weighted by volume, with SE given in parentheses.

parameters, for both chinook salmon and lake trout, can be found in Stewart et al. (1983), Beauchamp et al. (1989), and Hewett and Johnson (1992). For a summary of model applications, model performance, and model assumptions and sensitivities see Bartell et al. (1986), Ney (1990, 1993), and Brandt et al. (1992).

To implement the model, the energy density of predator and prey must be known. Energy density for chinook salmon was 2445 $cal \cdot g^{-1}$ (10 237 $J \cdot g^{-1}$) wet weight (Hewett and Johnson 1992) and for lake trout was 2922 $cal \cdot g^{-1}$ (12 208 $J \cdot g^{-1}$) wet weight (Hewett and Johnson 1992). Prey fish energy density was assumed to be 1800 $cal \cdot g^{-1}$ (7531 $J \cdot g^{-1}$) wet weight (Flath and Diana 1985) and was kept constant for all prey species for both lakes.

Growth rate potential was determined for each cell for all transects. A mean growth rate potential was then calculated providing a single value for habitat quality for each transect. The overall mean growth rate potential was calculated from the means of the transects for each lake. The proportion of the lake sampled capable of supporting a postive growth rate potential was determined for all transects combined for each lake.

Results

In general, growth rate potential for both chinook salmon and lake trout was highest near the metalimnion ($10 < T < 16°C$) but prey fish densities were generally highest in the epilimnion and lowest in the hypolimnion (Table 2, Figs. 2 and 3). The optimal temperature for chinook salmon (11–12°C) and lake trout (10.9°C) growth rates occurred along a narrow band in the metalimnion (Figs. 2 and 3).

Temperature and prey fish distribution

Both Lakes Michigan and Ontario were thermally stratified. Water temperatures ranged from 3.9 to 20.0°C in Lake Michigan and from 3.9 to 22.2°C in Lake Ontario (Fig. 4). Lake Michigan had a greater percentage of its water volume at 4°C, about 54% compared with Lake Ontario's 47%. Water temperatures greater than 20°C, the temperatures at which chinook salmon growth rate is always negative, comprised less than 0.1% of the total volume in Lake Michigan and about 10% of the total volume in Lake Ontario.

Prey fish biomass density ranged from 0 to 194 $g \cdot m^{-3}$ (mean 0.134 $g \cdot m^{-3}$) in Lake Michigan and from 0 to 214 $g \cdot m^{-3}$ (mean 0.142 $g \cdot m^{-3}$) in Lake Ontario. In general, the frequency distribution of prey fish biomass density was negative binomial. Overall, 91 and 92% of the environment sampled in Lakes Michigan and Ontario, respectively, contained no or very few prey fish, <0.05 $g \cdot m^{-3}$; regions with higher prey density were relatively rare.

Mean prey fish density varied from transect to transect and between lakes (Table 2). Highest mean fish densities occurred in the epilimnion ($T \geq 16°C$), whereas, lowest densities of fish generally occurred in the hypolimnion ($T \leq 10°C$) for both lakes. The highest proportion of prey fish occurred in waters warmer than 17°C in both lakes (Fig. 5). The highest biomass density of prey fish occurred at 18°C in Lake Michigan and at 21°C in Lake Ontario. At water temperatures ≤7°C, prey fish are present in Lake Michigan but absent or very rare in Lake Ontario (Fig. 5).

The proportion of the total water volume sampled among transects that was occupied by prey fish was similar for Lakes Michigan (21–39%) and Ontario (23–40%). Despite differences between lakes in hypolimnetic prey fish densities and spatial distributions, the proportion of volume occupied by prey in the hypolimnion was similar; 15–30% in Lake Michigan and 12–29% in Lake Ontario. However, differences between lakes occurred in both the metalimnion and epilimnion. In Lake Michigan, 98–100% of the total volume of the metalimnion was occupied by prey fish compared with 26–64% in Lake Ontario. The opposite was true for the epilimnion where the greatest proportion of occupied space occurred in Lake Ontario (59–87%) compared with Lake Michigan (40–60%).

Fig. 2. Two-dimensional visualization of (*a*) water temperature, (*b*) prey fish biomass density, (*c*) growth rate potential of a 5-kg chinook salmon, and (*d*) growth rate potential of a 4-kg lake trout along an acoustic transect for the Two Rivers region of Lake Michigan. Color scale is linear for all but the spatial distribution of prey fish density where data are presented on a logarithmic (base 10) scale.

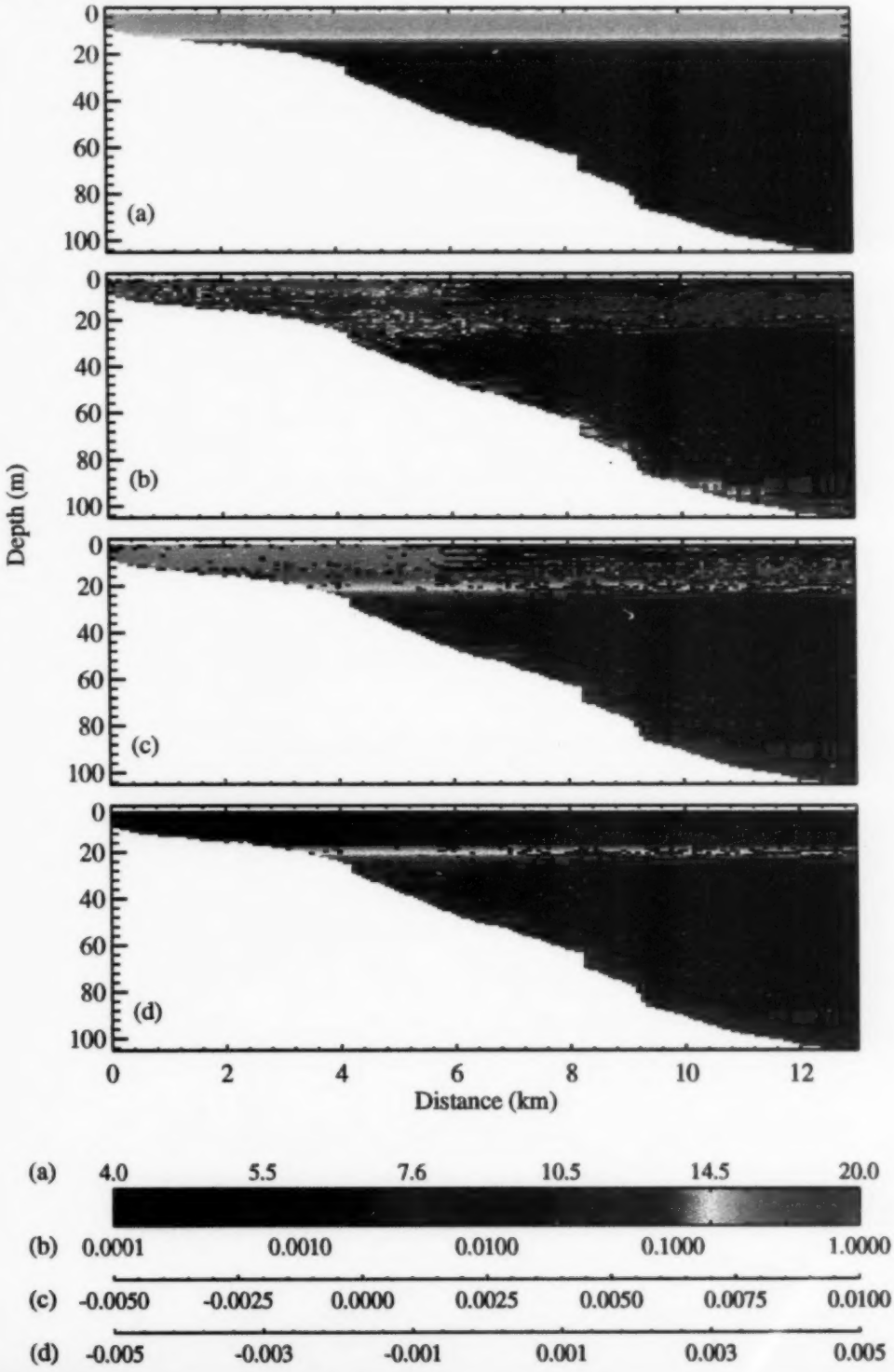
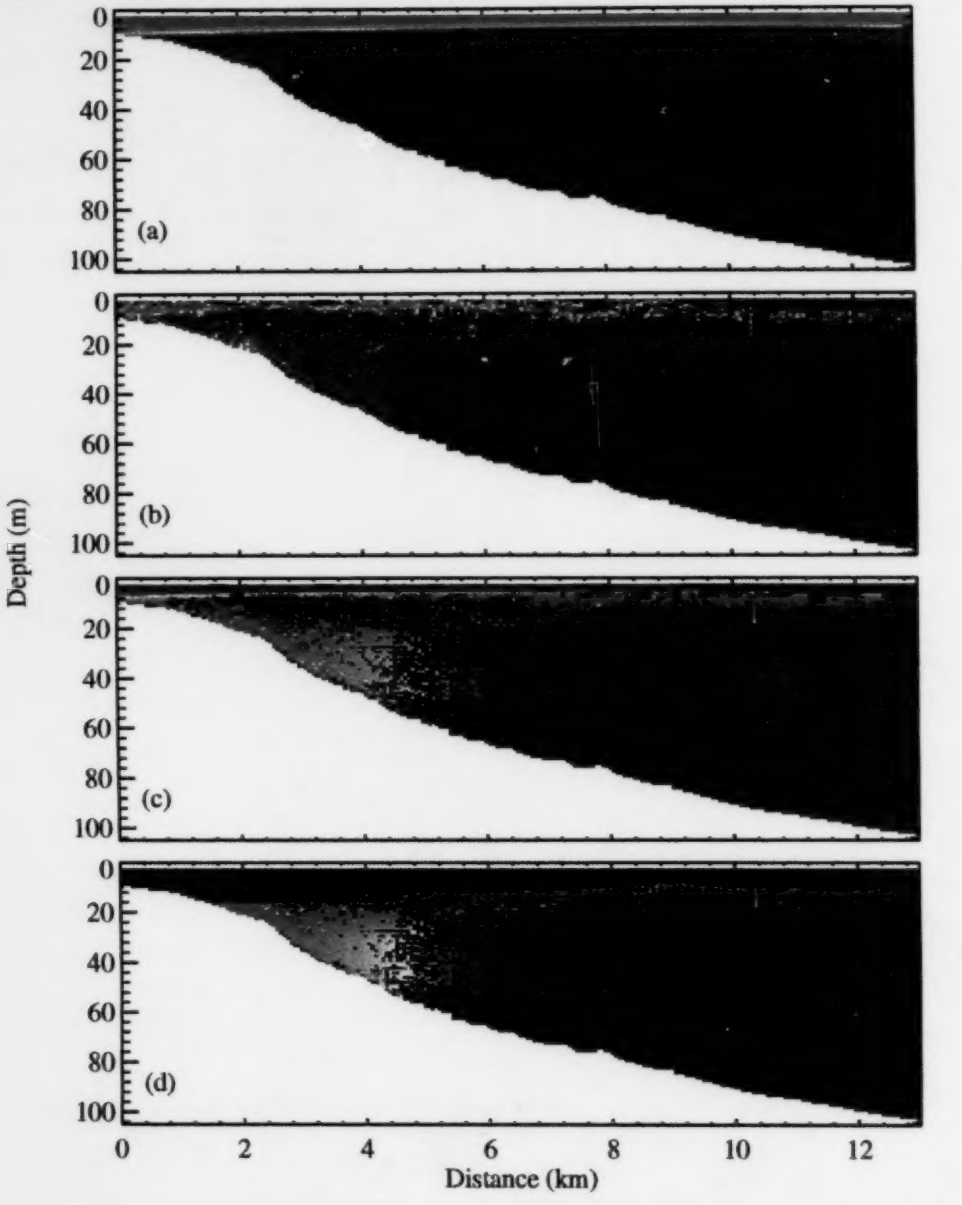
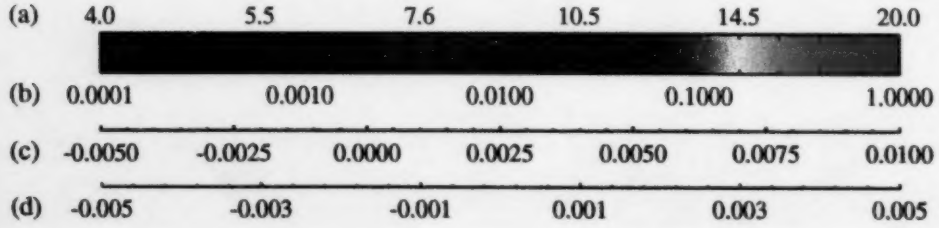


Fig. 3. Two-dimensional visualization of the Port Weller region of Lake Ontario. The arrangement is as in Fig. 2.





Chinook salmon growth rate potential

For both lakes, chinook salmon growth rate potential was highest within the metalimnion reflecting optimal temperatures for growth and intermediate prey concentrations. However, differences in growth rate potential between lakes occurred in colder waters ($T \leq 6°C$) and in the warmest waters ($T \geq 16°C$) (Figs. 2 and 3). In Lake Michigan, prey fish at temperatures ≤6°C supported minimal positive growth rate potential compared with the negative growth rate potentials occurring at similar water temperatures in Lake Ontario (Figs. 2 and 3). Furthermore, growth rate potential in Lake Michigan was generally positive in the epilimnion when prey fish were available (Fig. 2). However, for Lake Ontario, water temperatures in the epilimnion often exceeded 20°C and generally could not support positive growth rate potentials even when high prey fish concentrations were present (Fig. 3).

The overall quality of the pelagic environment for chinook salmon was similar between Lakes Michigan and Ontario. Lake-wide mean growth rate was 0.000 66 ± 0.000 986 $g \cdot g^{-1} \cdot d^{-1}$ (mean ± SD; $n = 5$) in Lake Michigan and −0.000 18 ± 0.000 734 $g \cdot g^{-1} \cdot d^{-1}$ ($n = 3$) in Lake Ontario. Means were not significantly different between lakes ($P > 0.20$). Overall, 26% (range 19–37%) of the Lake Michigan pelagic environment and 19% (range 10–25%) of the Lake Ontario pelagic environment could support positive growth rate potentials with a dominate peak in the frequency distribution of the growth rate potential occurring at 0 $g \cdot g^{-1} \cdot d^{-1}$ (Fig. 6).

Lake trout growth rate potential

The analysis of habitat quality for lake trout only includes the range of temperature from 3.9 to 10.9°C (as per Stewart et al. 1983). The greatest growth rate potential generally occurred at 10.9°C near the thermocline–bottom intersection and extended offshore along the bottom of the thermocline (Figs. 2 and 3).

The overall quality of the pelagic environment for lake trout was similar between Lakes Michigan and Ontario. Lake-wide mean growth rate was −0.000 23 ± 0.000 093 $g \cdot g^{-1} \cdot d^{-1}$ ($n = 5$) in Lake Michigan and −0.000 15 ± 0.000 143 $g \cdot g^{-1} \cdot d^{-1}$ ($n = 3$) in Lake Ontario. Means were not significantly different between lakes ($P > 0.10$). Overall, only 21% (range 15–30%) of the Lake Michigan hypolimnetic environment and 19% (range 10–22%) of the Lake Ontario hypolimnetic environment could support positive growth rate potentials (Fig. 7). As with chinook salmon growth rate potential, the dominate peak in the frequency distribution of lake trout growth rate potential occurred at 0 $g \cdot g^{-1} \cdot d^{-1}$ (Fig. 7).

Discussion

Mean growth rate potential is used as an index of habitat quality for the total pelagic habitat from the fishes' perspective. As such, the measure includes regions in the environment that predator fish may not occupy and is a measure of the habitat and not the fish. By considering the total pelagic habitat, an evaluation is possible without the need for considering predator distributions and provides a standard for comparisons amongst ecosystems.

Fig. 4. Histogram of the proportion of the sampled lake volume at each temperature interval in Lake Michigan August–September 1987 (solid line) and Lake Ontario July–August 1990 (broken line).

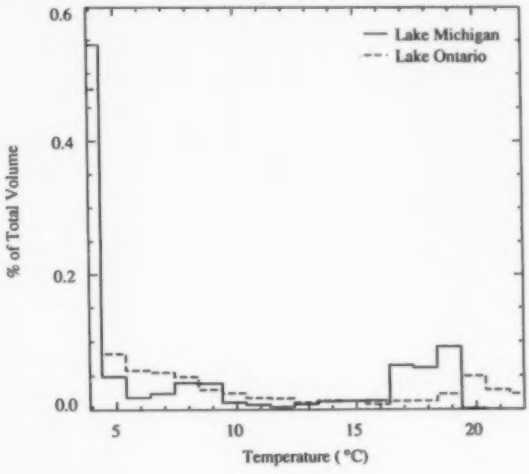
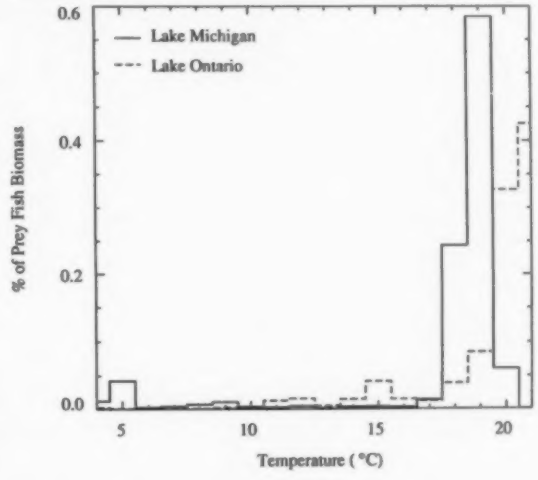


Fig. 5. Histogram of the proportion of the total lake volume at specified prey fish density ($g \cdot m^{-3}$) in Lake Michigan August–September 1987 (solid line) and Lake Ontario July–August 1990 (broken line).



Chinook salmon

The overall quality of the summer pelagic habitat for chinook salmon, as defined by the mean growth rate potential, appeared to be similar between Lake Michigan in 1987 and Lake Ontario in 1990. However, Lake Michigan provided a greater volume of water that supported positive growth rate potential than Lake Ontario. Differences in the spatial arrangement of growth rate potential of Lake Michigan and Lake Ontario environments reflect both differences in the thermal structure and the spatial distribution

Fig. 6. Histogram of the distribution of chinook salmon growth rates for (*a*) the entire range of growth rates modeled, and for (*b*) the range of positive growth rates in Lake Michigan August–September 1987 (solid line) and Lake Ontario July–August 1990 (broken line).

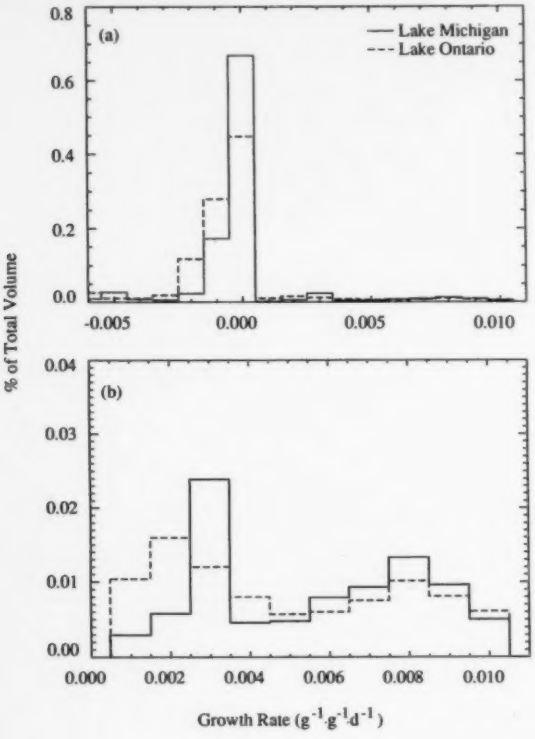
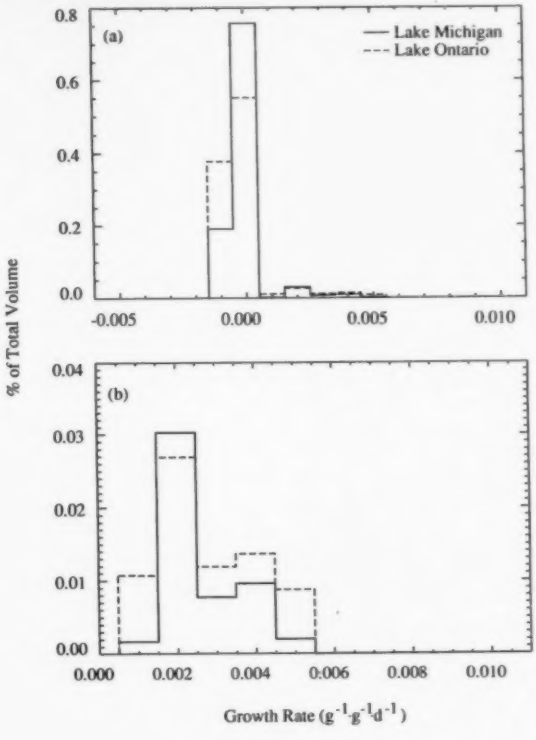


Fig. 7. Histogram of the distribution of lake trout growth rates for (*a*) the entire range of growth rates modeled, and for (*b*) the range of positive growth rates in Lake Michigan August–September 1987 (solid line) and Lake Ontario July–August 1990 (broken line).



of prey fish. In Lake Ontario, most of the prey fish biomass is found in waters warmer than 20°C, temperatures which cannot support positive chinook salmon growth. In Lake Michigan, however, the higher prey densities occur in water temperatures less than 20°C and are capable of supporting high growth rates of chinook salmon.

Differences in epilimnetic water temperatures between Lake Michigan (1987) and Lake Ontario (1990) appear to be real and not an artifact of the particular years sampled. The median (minimum and maximum) surface temperature for Lake Michigan on August 2, 1990, was 16.5°C (12.0°C, 20.5°C) (Bolgrien and Brooks 1992), whereas surface temperatures for Lake Ontario for the first week in August ranged from 20.0 to 22.2°C (this study). Typical surface water tempertures for Lake Ontario are warmer than 20°C in early August (Irbe 1992). Thus, it is likely that the temperatures observed for Lake Michigan and Lake Ontario in this study reflect actual differences and not just odd years.

Another important difference between the two lakes is the abundance of bloaters in water temperatures less than 10°C in Lake Michigan but the absence of bloaters from Lake Ontario. The abundance of bloaters effectively increases the overall quality of the hypolimnion in the Lake Michigan environment by providing a food resource and marginal positive growth rate potentials at temperatures <7°C.

Lake trout

The quality of the habitat for lake trout was similar between Lakes Michigan and Ontario. Both Lakes Michigan and Ontario had a similar proportion of the environment ($T \leq$ 10.9°C) occupied by prey fish, but the mean prey fish density was greater in Lake Michigan than in Lake Ontario. Given a random or uniform spatial distribution of prey fish, Lake Michigan would be expected to have a higher quality environment for lake trout because of the higher hypolimnetic prey fish density. However, the distribution of prey fish is not random. In Lake Ontario, the majority of prey fish occupied hypolimnetic waters ranging in temperature from 7 to 10.9°C, temperatures at which high growth rates of lake trout occur. For Lake Michigan, prey fish were distributed throughout the hypolimnion in water temperatures that ranged from 3.9 to 10.9·C. However, relatively high bloater densities in water temperatures <7°C support only minimal lake trout growth rates in Lake Michigan, whereas weight loss occurs at a very reduced rate for predators at temperatures <7°C with no prey fish in Lake Ontario.

Edwards et al. (1990), using literature data from 1964 to 1987, examined the quality of the environment for all five Great Lakes using lake trout as an indicator species. The categories examined included exploitation and production, biotic environment, abiotic environment, and contaminants. Overall, the habitat quality of Lakes Michigan and Ontario were similar. However, some differences existed between lakes in the above categories. Index scores from the analysis suggested that the abiotic environment was similar between the lakes, but the biotic environment (reflecting diet composition and quantity of food consumed) was better in Lake Michigan than Lake Ontario. However, contaminant concentrations and lake trout mortality were higher in Lake Michigan. Our independent analysis that considers habitat quality from the perspective of the fish suggested that the habitat quality of the lakes was similar despite differences in the prey fish community structure and thermal characteristics.

Model assumptions and research needs

Our conclusions are constrained by the uncertainty in the models, the apparent small field sample size, and the restriction to only one season and predator size class. Thus, interpretations may change with further developments in the model, increased sampling effort, and extension of the model across seasons and predator size classes.

Foraging model

The weakest link to quantify the quality of a fish's habitat is the transformation of measured prey fish density and prey fish size into an estimate of consumption rate for the calculation of growth rate potential (Bartell et al. 1986; D.M. Mason and S.B. Brandt, unpublished data). We assumed a constant reactive distance and a detection and capture probability of 1.0 in the foraging model. Undoubtedly, reactive distance will change in response to light levels (e.g., new moon vs. full moon) and turbidity (Wright and O'Brien 1984; Aksnes and Giske 1993; Gregory and Northcote 1993), while the probability of detection and capture will vary as a function of prey size, prey species, predator experience, satiation level, and predator preference (Stephens and Krebs 1986; Savitz and Bardygula 1989; Hughes et al. 1992). Light level at depth, prey size structure, prey species composition, and predator experience may differ between lakes and modify our results. Furthermore, predator and prey interactions are sensitive to a variety of stressors (e.g., contaminants) that influence prey vulnerability and depress predator feeding rates (Heath 1987; Beitinger 1990; Beitinger and McCauley 1990). Such affects have obvious implications for our comparisons of habitat quality of Lakes Michigan and Ontario if stressors differ between lakes. Future research should address behavioral interactions between salmonines and their prey, how the intensity of interaction varies with changes in the physical environment (e.g., temperature, light intensity), and the effects of stressors on predator and prey interactions.

Duration of foraging or foraging time is critically important in a foraging model (e.g., Walters and Juanes 1993). If the predator feeds continuously throughout the day, maximum daily consumption (ϕ_{max}) may be obtained for both high and low prey densities with satiation occurring more rapidly at high prey concentrations. However, if foraging is limited to specific feeding periods (e.g., dawn and dusk), total food consumed per day may diverge between low and high prey fish densities. Given a foraging interval less than assumed here, the estimate of growth rate potential in regions of low prey density would be reduced causing a decrease in the mean growth rate potential. Overall, prey fish densities are about three times higher in Lake Ontario than in Lake Michigan (A. Goyke, S.B. Brandt, and D.M. Mason, unpublished data, see footnote 3). Thus, mean growth rate potential may be less in Lake Michigan than calculated. Two potential modifications of our approach would be to (*i*) incorporate feeding periodicity and foraging duration of salmonine predators (e.g., Mason and Patrick 1993) and (*ii*) include a calculated "total time" necessary to obtain daily maximum ration for each cell in the model.

The use of nighttime prey fish distributions requires explanation beyond the recognition of data availability. Salmonines were assumed to forage at night. However, if salmonines forage during dawn and dusk periods, for a similar foraging duration, our conclusions would remain roughly the same. The spatial distribution of prey fish at night is a close approximation for prey fish distributions at early dawn and late dusk (e.g., Janssen and Brandt 1980). The feeding periodicity of salmonines is poorly understood, but some evidence suggests that salmonines may forage at night (Olson 1984; Heggenes et al. 1993). Furthermore, nighttime activity and foraging may be more important for diurnally active fishes than previously thought (e.g., Collins and Hinch 1993). Our analysis highlights the need for additional research on the feeding ecology of Great Lakes salmonines.

Bioenergetics model

Beyond the obvious contraint of species-specific parameterization of the bioenergetics model (e.g., Ney 1993), energy density (calories per gram) of prey fish has important implications for the interpretation of results. Energy density is size-specific, species-specific, and can vary seasonally (e.g., Stewart and Binkowski 1986; Hewett and Stewart 1989). Evidence exists suggesting that energy density may differ for alewife between Lakes Michigan and Ontario (Rand et al. 1995). Furthermore, there are differences in energy density among size classes of alewife and among alewife, bloater, and rainbow smelt (Stewart et al. 1983; Rudstam et al. 1994). If the mean estimate of prey fish energy density were too high, this would provide a measure of habitat quality that is too high. Further applications of this approach must consider potential differences in energy density among prey species, changes in energy density over time, and the spatial arrangement of prey fish by species.

Increasing the spatial extent of the field samples beyond the 100-m bathymetric contour in both lakes may provide additional information and modify the present measure of habitat quality. For example, alewife and rainbow smelt in Lake Ontario have nighttime summer distributions that extend across the lake with densities in mid-lake that often exceed 1.0 $g \cdot m^{-3}$ (A. Goyke, S.B. Brandt, and D.M. Mason, unpublished data, see footnote 3). But in Lake Michigan, the nighttime densities of alewife, bloater, and rainbow

smelt beyond the 100-m bathymetric contour are generally very low (Brandt et al. 1991). Sampling pelagic waters beyond the 100-m bathymetric contour may increase the estimate of the quality of the Lake Ontario environment for chinook salmon but decrease the estimate of habitat quality in Lake Michigan.

Despite present model limitations, the spatially explicit approach provides a solid foundation for evaluating species-specific habitat needs based on the physiological requirements of reference species. Our approach provides information on the physiological response of fishes that cannot be determined from measures of prey abundance, prey size, or water temperature alone. Furthermore, complex spatial information of both the physical and biological environment is explicitly considered for the evaluation of habitat quality. More extensive geographical coverage and increased sample sizes are now collected by federal (United States and Canada) and state agencies throughout the Great Lakes during annual prey fish assessments. Data from these monitoring programs can provide the information required for quantifying and monitoring change in habitat quality over time with respect to reference species. Expanding our functional definition of habitat quality to include seasonal and ontogenetic affects should be considered for quantifying seasonal and ontogenetic bottlenecks in habitat quality. In addition, new techniques that consider the spatial complexities within and between transects (e.g., Whitehead and Walde 1992) need to be developed to detect true differences between ecosystems.

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References

Aksnes, D.L., and J. Giske. 1993. A theoretical model of aquatic visual feeding. Ecol. Modell. 67: 233–250.

Bartell, S.M., J.E. Breck, R.H. Gardner, and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetic models. Can. J. Fish. Aquat. Sci. 43: 160–168.

Beauchamp, D.A., D.J. Stewart, and G.L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. Trans. Am. Fish. Soc. 118: 597–607.

Beitinger, T.L. 1990. Behavioral reactions for the assessment of stress in fishes. J. Great Lakes Res. 16: 495–528.

Beitinger, T.L., and R.W. McCauley. 1990. Whole-animal physiological processes for the assessment of stress in fish. J. Great Lakes Res. 16: 542–575.

Bolgrien, D.W., and A.S. Brooks. 1992. Analysis of thermal features of Lake Michigan from AVHRR satellite images. J. Great Lakes Res. 18: 159–266.

Brandt, S.B. 1986. Food of trout and salmon in Lake Ontario. J. Great Lakes Res. 12: 200–205.

Brandt, S.B., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in the Chesapeake Bay. Trans. Am. Fish. Soc. 122: 845–869.

Brandt, S.B., D.M. Mason, E.V. Patrick, R.L. Argyle, L. Wells, P. Unger, and D.J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Can. J. Fish. Aquat. Sci. 48: 894–908.

Brandt, S.B., D.M. Mason, and E.V. Patrick. 1992. Spatially-explicit models of fish growth rate. Fisheries (Bethesda, Md.), 17(2): 23–35.

Burczynski, J.J., and R.L. Johnson. 1986. Application of dual-beam acoustic survey techniques to limnetic populations of juvenile sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 43: 1776–1788.

Burczynski, J.J., P.H. Michaletz, and G.M. Marrone. 1987. Hydroacoustic assessment of the abundance and distribution of rainbow smelt in Lake Oahe. N. Am. J. Fish. Manage. 7: 106–116.

Collins, N.C., and S.G. Hinch. 1993. Diel and seasonal variation in foraging activities of pumpkinseeds in an Ontario pond. Trans. Am. Fish. Soc. 122: 357–365.

Costanza, R. 1992. Towards an operational definition of ecosystem health, p. 239–256. *In* R. Costanza, B.G. Norton, and B.D. Haskell [ed.] Ecosystem health: new goals for environmental management. Island Press, Washington, D.C.

Costanza, R., B.G. Norton, and B.D. Haskell [Ed]. 1992. Ecosystem health: new goals for environmental management. Island Press, Washington, D.C.

Eck, G.W., and L. Wells. 1987. Recent changes in Lake Michigan's fish community and their probable causes, with emphasis on the role of the alewife (*Alosa pseudoharengus*). Can J. Fish. Aquat. Sci. 44(Suppl. 2): 53–60.

Edwards, C.J., R.A. Ryder, and T.R. Marshall. 1990. Using lake trout as a surrogate of ecosystem health for oligotrophic waters of the Great Lakes. J. Great Lakes Res. 16: 591–608.

Elrod, J.H. 1983. Seasonal food of juvenile lake trout in U.S. waters of Lake Ontario. J. Great Lakes Res. 9: 396–402.

Evans, M.S. 1990. Large lake responses to declines in the abundance of major fish predator: the Lake Michigan example. Can J. Fish. Aquat. Sci. 47: 1738–1754.

Flath, L.E., and J.S. Diana. 1985. Seasonal energy dynamics of the alewife in southeastern Lake Michigan. Trans. Am. Fish. Soc. 114: 328–337.

Foote, K.G. 1990. Spheres for calibrating an eleven-frequency acoustic measurement system. J. Cons. Cons. Int. Explor. Mer, 46: 284–286.

Foote, K.G., H.P. Knudsen, G. Vestnes, D.N. MacLennan, and E.J. Simmonds. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. Coop. Res. Rep. Cons. Int. Explor. Mer, 144: 69 p.

Gerritsen, J., and J.R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. J. Fish. Res. Board Can. 34: 73–82.

Goyke, A., and S.B. Brandt. 1993. Spatial models of salmonine growth rates in Lake Ontario. Trans. Am. Fish. Soc. 122: 870–883.

Gregory, R.S., and T.G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Can. J. Fish. Aquat. Sci. 50: 233–240.

Hagar, J. 1984. Diets of Lake Michigan salmonids: an assessment of the dynamics of predator–prey interactions. M.S. Thesis, University of Wisconsin, Madison, Wis. 97 p.

Hansen, M.J., P.T. Schultz, and B.A. Lasee. 1990. Changes in Wisconsin's Lake Michigan salmonid sport fishery, 1969–1985. N. Am. J. Fish. Manage. 10: 442–457.

Heath, A.G. 1987. Water pollution and fish physiology. CRC Press, Ann Arbor, Mich. 245 p.

Heggenes, J., O.M.W. Krogg, O.R. Lindas, J.G. Kokk, and T. Bremnes. 1993. Homeostatic behavioral responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. J. Animal Ecol. 62: 295–308.

Hewett, S.W., and B.L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. Univ. Wisc. Sea Grant Tech. Rep. WIS-SG-87-245.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics 2: a generalized bioenergetics model of fish growth for microcomputers. Univ. Wisc. Sea Grant Tech. Rep. WIS-SG-92-250.

Hewett. S.W., and D.J. Stewart. 1989. Zooplanktivory by alewives in Lake Michigan: ontogenetic, seasonal and historical patterns. Trans. Am. Fish. Soc. 118: 581–596.

Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symp. 2: 17–29.

Hughes, R.N., M.J. Kaiser, P.A. Mackney, and K. Warburton. 1992. Optimizing foraging behavior through learning. J. Fish Biol. 41(Suppl. B): 77–91.

Irbe, G.J. 1992. Great Lakes surface water temperature climatology. Environment Canada, Atmospheric Environment Service, Ottawa, Ont. Climatol. Stud. 43: 215 p.

Janssen, J., and S.B. Brandt. 1980. Feeding ecology and vertical migration of adult alewives (*Alosa pseudoharengus*) in Lake Michigan. Can. J. Fish. Aquat. Sci. 37: 177–184.

Jones, M.D., D.J. Stewart, R. O'Gorman, E. Mills, O. Johannsson, and W.G. Sprules. 1992. Status of the Lake Ontario offshore pelagic fish community and related ecosystem in 1992. Report prepared at the request of the Lake Ontario Committee of the Great Lakes Fishery Commission. 34 p.

Jude, D.J., and F.J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michgan. Can. J. Fish. Aquat. Sci. 42: 1154–1157.

Jude, D.J., FJ. Tesar, S.F. Deboe, and T.J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Trans. Am. Fish. Soc. 116: 677–691.

Keller, M., K.D. Smith, and R.W. Rybicki [Ed]. 1989. Summary of salmon and trout management in Lake Michigan. Mich. Dep. Nat. Resour. Fish. Tech. Rep. 89-1: 27 p.

LeTendre, G.C., and P.J. Savoie. 1992. Lake Ontario stocking and marking program for 1991. Section 15 in Lake Ontario Fisheries Unit 1991 Annual Report. Ontario Ministry of Natural Resources, Glenora, Ont.

Love, R.H. 1977. Target strength of an individual fish at any aspect. J. Acoust. Soc. Am. 62: 1397–1403.

Luo, J,. and S.B. Brandt. 1993. Bay anchovy *Anchoa mitchilli* production and consumption in mid-Chesapeake Bay based on a bioenergetics model and acoustic measures of fish abundance. Mar. Ecol. Prog. Ser. 98: 223–236.

Mason, D.M., and E.V. Patrick. 1993. A model for the space–time dependence of feeding for pelagic fish populations. Trans. Am. Fish. Soc. 122: 884–901.

McComish, T.S. 1989. Changes in salmonine predator–prey relationships in extreme southern Lake Michigan. Illinois–Indiana Sea Grant Rep. IL-IN-SG-R-89-2. 10 p.

Monteleone, D.M., and E.D. Houde. 1990. Influence of maternal size on survival and growth of striped bass (*Morone saxatilis* Walbaum) eggs and larvae. J. Exp. Mar. Biol. Ecol. 140: 1–11.

Ney, J.J. 1990. Trophic economies in fisheries: assessment of demand–supply relationships between predators and prey. Rev. Aquat. Sci. 2: 55–81.

Ney, J.J. 1993. Bioenergetics today: growing pains on the cutting edge. Trans. Am. Fish. Soc. 122: 736–748.

Olson, R.A. 1984. Summer resource utilization by salmonids and their prey in Lake Ontario. M.S. Thesis. State University of New York, Fredonia, N.Y.

Pepin, P., and R.A. Myers. 1991. Significance of eggs and larval size to recruitment variability of temperature marine fish. Can. J. Fish. Aquat. Sci. 48: 1820–1828.

Powell, L., and T.K. Stanton. 1983. A programmable microcomputer-based sonar echo processor. IEEE J. Ocean Eng. OE-E8(4): 280–287.

Rand, P.S., D.J. Stewart, B.F. Lantry, L.G. Rudstam, O.E. Johansson, A.P. Goyke, S.B. Brandt, R. O'Gorman, and G.W. Eck. 1995. Effect of lake-wide planktivory by the pelagic community in Lakes Ontario and Michigan. Can. J. Fish. Aquat. Sci. 52: 1546–1563.

Rudstam, L.G., J.J. Magnuson, and W.T. Tonn. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. Can. J. Fish. Aquat. Sci. 41: 1252–1255.

Rudstam, L.G., F.P. Binkowski, and M.A. Miller. 1994 A bioenergetics model for the analysis of food consumption patterns by bloater in Lake Michigan. Trans. Am. Fish. Soc. 123: 344–357.

Ryder, R.A. 1990. Ecosystem health, a human perception: definition, detection, and the dichotomous key. J. Great Lakes Res. 16: 619–624.

Savitz, J., and L. Bardygula. 1989. Analysis of the behavioral bases for changes in salmonid diets. Illinois–Indiana Sea Grant Rep. IL-IN-SG-R-89-3: 29 p.

Stephens, D.W., and J.R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

Stewart, D.J., and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. 115: 643–661.

Stewart, D.J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Can. J. Fish. Aquat. Sci. 48: 909–922.

Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fish and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

Stewart, D.J., D.W. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40: 681–698.

Talhelm, D.R. 1988. Economics of Great Lakes fisheries: a 1985 assessment. Great Lakes Fish. Comm. Tech. Rep. 54.

Thorne, R.E. 1983. Assessment of population abundance by hydroacoustics. Biol. Oceanogr. 2: 253–262.

Traynor, J.J., and J.E. Ehrenberg. 1979. Evaluation of the dual-beam acoustic fish target strength method. J. Fish. Res. Board Can. 36: 1065–1071.

Walters, C.J., and F. Juanes. 1993. Recruitment limitations as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Can. J. Fish. Aquat. Sci. 50: 2058–2070.

Whitehead, H., and S.J. Walde. 1992. Habitat dimensionality and mean search distances of top predators: implication for ecosystem structure. Theor. Popul. Biol. 42: 1–9.

Wright, D.I., and W.J. O'Brien. 1984. The development and field test of a tactical model of the planktivorous feeding white crappie (*Pomoxis annularis*). Ecol. Monogr. 54: 65–98.

Zastrow, C.E., E.D. Houde, and E.H. Saunders. 1989. Quality of striped bass (*Morone saxatilis*) eggs in relation to river source and female weight. Rapp. P.-V. Reun. Cons. Int. Explor. Mer, 191: 34–42.

PERSPECTIVE

Toward a definition of conservation principles for fisheries management

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Abstract: Conservation, like beauty, is clearly in the eye of the beholder. The lack of a clear definition of what is meant by the term conservation, however, may encourage misconceptions about the degree to which biological objectives can be traded off against pressing economic and social objectives. Our purpose is to promote a dialogue about the meaning and practice of conservation, which might lead toward consensus on essential biological objectives. We present a brief history of the philosophical evolution of the term conservation and offer a definition of conservation based on the argument for an ecological ethic. This ethic requires that human benefits be derived in a sustainable manner and recognizes that human uses need to be reconciled with intrinsic and necessary ecosystemic functions and structures. We then present a preliminary set of operating principles applicable to the management of fish stocks that are consistent with an ecological or ecosystemic view of conservation. By proposing a set of conservation principles for fisheries management we hope to initiate a debate about just what those principles ought to be.

Résumé : La conservation, comme la beauté, est dans l'oeil de celui qui regarde. Toutefois, l'absence d'une définition claire de ce qu'on entend par le terme conservation peut causer des malentendus quant à la possibilité de compromis entre les objectifs biologiques et des objectifs économiques et sociaux pressants. Le but du présent article est de promouvoir un dialogue sur la signification et la pratique de la conservation, ce qui pourrait amener à un consensus sur les objectifs biologiques essentiels. Nous présentons un bref historique de l'évolution philosophique du terme conservation et offrons une définition de la conservation fondée sur la justification d'une éthique écologique; cette éthique exige que les humains adoptent des pratiques durables et reconnaît que les utilisations humaines doivent concorder avec les fonctions et structures intrinsèques et nécessaires des écosystèmes. Nous présentons ensuite une série préliminaire de principes opérationnels qui sont applicables à la gestion des stocks de poissons et concordent avec une perspective écologique ou écosystémique de la conservation. En proposant ces principes de conservation, nous espérons lancer le débat sur ce que devraient être de tels principes.
[Traduit par la Rédaction]

Introduction

A dynamic interplay among biological, economic, and social objectives has, and will, determine the fate of Canada's fisheries resources. Conservation and protection are the central features of any definition of biological objectives, while efficiency and allocation issues dominate the definition of economic and social objectives. Parsons (1993) has reviewed the historical conflict among these objectives and the influence of that conflict on the evolution of fisheries management practice in Canada. This evolution has been marked by recent attempts to enshrine biological objectives in law. In 1985, the federal government amended the Fisheries Act by adding a statement of purposes (cf. Parsons 1993). The first purpose is "to provide for the conservation and protection of fish and waters frequented by fish."

The conservation and allocation of fisheries resources in Canada are also subject to the 1990 Supreme Court of Canada decision (*Regina v. Sparrow* 1990). While this decision established the priority of food fishery rights of indigenous peoples over the rights of other users, it also established the primacy of conservation needs over any use (aboriginal or not). Unfortunately, *Regina v. Sparrow* did not specify what conservation means, nor did it provide

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guidance on how to determine when conservation needs are met.

Although the courts have repeatedly reaffirmed the federal government's responsibility for conservation (Parsons 1993), no federal government agency has, to our knowledge, adopted a formal definition of conservation for fisheries resources. Our concern, shared by Parsons (1993), is that the lack of a clear definition of conservation may foster misconceptions about the degree to which biological objectives can be safely traded off against pressing economic and social objectives. Our purpose is to promote a dialogue about the meaning and practice of conservation, in the hope that this will lead toward consensus on essential biological objectives. We begin with a brief exploration of the philosophical evolution of the term conservation. Then we offer a definition of conservation based on the argument for an ecological ethic. Following the definition, we present a preliminary set of operating principles applicable to the management of fish stocks, principles consistent with an ecological, or ecosystemic, view of conservation.

The principles espoused in this paper are intended to apply mainly to areas in which self-sustaining aquatic ecosystems are the norm. This includes, for example, most of Canada except heavily urbanized regions and regions subject to intensive agriculture where aquatic ecosystems may have been severely altered "by one or more of a score of human or anthropogenic practices deleterious to the more preferred species of fish" (Regier 1976).

A brief philosophical history of conservation

Reviews by Pepper (1984), Callicott (1991), and Norton (1991) provide detailed summaries of the environmentalist view of conservation, as it evolved in the West over the last 200 years. North American usage of this term has been shaped by three ethical precepts: the prescientific Romantic–Transcendental Preservation Ethic of Ralph Waldo Emerson, Henry David Thoreau, and John Muir; the Resource Conservation Ethic of Gifford Pinchot; and the Evolutionary–Ecological Land Ethic of Aldo Leopold (Callicott 1991).

The Romantic–Transcendental Preservationists believed that nature was the proper source of religion. This line of thought runs back to Classical Greece (Boas 1973; Pepper 1984) and partly inspired the romantic movement of the 18th and 19th centuries. Its founders included Rousseau, who argued that the inherent goodness of nature and humanity were inseparable, and Carlyle, Coleridge, and Wordsworth, who each promoted pantheistic themes wherein the natural world was the source of true spiritual knowledge (Baumer 1973; Boas 1973; Pepper 1984). In the New World, Emerson and Thoreau wrote about the connection between nature and the psychological health of mankind. They argued for the intrinsic value of wilderness as a place of beauty, quiet contemplation, and spiritual renewal. Building on these ideas, the strong preservationist wing of the environmental movement emerged. The first leader of this movement was John Muir, wilderness writer and first president of the Sierra Club.

Gifford Pinchot, Chief of the U.S. Forest Service from 1898 to 1910, was the leader of the utilitarian school of early environmentalists and helped to formulate the policies that became known as the conservation movement. Until the early 1900s, the public had never heard of the term conservation, but through President Theodore Roosevelt, it became the "label of a national issue" (Leopold 1933). The new policy was defined as "the use of the natural resources for the greatest good of the greatest number for the longest time" (Pinchot 1947). This phrase is probably the progenitor of the maxim "conservation through wise use," or simply "wise use," a term that Pinchot himself used (Pinchot 1947). According to Nash (1969), Pinchot and his colleagues appropriated the term conservation for the wise-use movement.[1] Pinchot's secular, utilitarian view of conservation, with its dual principles of equity and efficiency (Callicott 1991), became the basis for the Resource Conservation Ethic.

Pinchot's view of conservation led to conflict with the preservationists, and particularly with John Muir. A disagreement between them in 1897 over the use of forest preserves (later called National Forests), and a long and acrimonious battle some years later over the building of a dam in Yosemite National Park, produced a permanent split in the leadership of the nascent conservation movement. Two distinct and intractable schools of thought were established, each claiming exclusive rights to the meaning of the term conservation, and each accusing the other of being "false standard bearers of the gospel" (Hays 1959).

These conflicting views on the meaning of conservation are also evident in early literature on the subject in Canada. Canadian participation in Roosevelt's North American Conservation Conference led directly to the establishment of the Commission of Conservation of Canada in May 1909 (Sifton 1910). In the public minutes of this group, the meaning of conservation slides back and forth between protection and wise use, with the Dominion entomologist Gordon Hewitt (1918) echoing Pinchot's view ("the real idea of conservation; use without abuse") and the Chairman of the Commission, Clifford Sifton (1910), being very careful to draw a line between "effective conservation" of resources and their "economical use."

Today, the most powerful and influential private conservation organizations represent the interests of preservationists and thus "remain firmly rooted in the prescientific Romantic–Transcendental intellectual complex." In contrast, government resource agencies "are still very much ruled by the 19th century Resource Conservation Ethic" (Callicott 1991). Thus, current events are still influenced by the internecine conflicts of the 1890s.

Aldo Leopold developed an alternative to the strict preservationist and utilitarian viewpoints. His understanding of conservation evolved beyond his early practice of wise use because of his interest in ecology and his seminal activities in the emerging field of wildlife management.

[1] Not to be confused with a loose amalgam of some 250 disparate groups associated under the name Wise Use or Wise Use Movement created in the late 1980s, whose express purpose is to destroy the environmental movement (Krakauer 1991).

Leopold (1939) suggested that economic biology, with its focus on providing a competitive advantage to "useful" species, needed to be replaced by an ecological approach that conceived of the biota as a single system, the land organism, "so complex, so conditioned by interwoven cooperations and competitions, that no man can say where utility begins or ends." The purpose of conservation was to perpetuate the health of this system. Health was simply "the capacity of the land for self-renewal" and conservation "our effort to understand and preserve this capacity" (Leopold 1949).

Leopold based his view of conservation on two complementary principles: first, that humanity is best served by preserving the natural life support systems of the planet; second, that indigenous ecological systems have intrinsic value that must be respected. He built an ecological rationale for his views that avoided the largely untenable sentimentalism of the Romantics and the strictly anthropocentric utilitarianism of the advocates of wise use. His ideas found eloquent advocates in Canada (e.g., Clarke 1963; Coventry 1963).

The evolutionary–ecological land ethic of Leopold is grounded in an intimate appreciation of the interconnected structures and functions of ecosystems and their vulnerability to unguarded tinkering. Since Leopold's time, the land ethic has evolved into the concept of the ecosystem approach (Christie et al. 1986), which aims to balance ecological, economic, and social objectives and recognizes that human uses must be reconciled with intrinsic and necessary ecosystemic functions and structures.

Miller (1986), Regier and Bronson (1992), and others have further attempted to recognize and codify the range of thinking exemplified by the preservationist and utilitarian attitudes. Miller (1986) describes the divergent viewpoints that are generally represented in environmental disputes as technocratic (=utilitarian) and humanistic (=preservationist). These are ideological perspectives that cannot be resolved by scientific validation and rational debate.

Both the preservationist and utilitarian approaches to conservation have weaknesses. Both represent anthropocentric views of ecosystems. The former focuses on meeting the aesthetic and spiritual needs of humans while the latter focuses on meeting their material needs. Extreme preservationist attitudes promote intrinsic valuation of resources and view wild ecosystems as temporally static, rather than naturally dynamic. Extreme utilitarian attitudes promote monetary valuation of resources and view ecosystems as collections of organisms that can be arranged and rearranged at will. Science cannot be used to determine how resources should be valued in either case; however, science can provide objective validation of those assumptions about the real world that underlie any particular valuation procedure. Current ecological science presents a view of ecosystems (e.g., Pimm 1991: systems of interacting biological populations, characterized by temporal variation in abundance and species composition that are constrained by past and present environmental conditions and competitive–predatory linkages) that is quite incompatible with either of the ideological positions outlined above.

In the modern parlance of resource management, the terms sustainable development, sustainable use, and conservation are often used interchangeably in ways that are strongly influenced by the wise-use ethic of Pinchot. The original definition of sustainable development, "development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (World Commission on Environment and Development 1987), is really wise use with a longer time horizon. A recent redefinition ("improving the quality of human life while living within the carrying capacity of supporting ecosystems" World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991) moves a bit towards Leopold's position by explicitly recognizing the existence of ecological limits on use. Sustainable use ("use of an organism, ecosystem or other renewable resource at a rate within its capacity for renewal" World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991) focuses directly on use, but recognizes that limits on use should be based on resource renewal rates rather than existing inventory levels.

Several recent definitions of conservation also have a strong utilitarian focus. In 1980, the World Conservation Strategy of the International Union for the Conservation of Nature and Natural Resources (1980) defined conservation as "the management of human *use* [our italics] of the biosphere so that it may yield the greatest sustainable benefit to present generations while maintaining its potential to meet the needs and aspirations of future generations." In 1991, conservation was defined as "the management of human *use* [our italics] of organisms or ecosystems to ensure such use is sustainable. Besides sustainable use, conservation includes protection, maintenance, rehabilitation, restoration, and enhancement of populations and ecosystems" (World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991).

The principal focus of all these definitions is resource use. There are many reasons for rejecting use, or wise use as the main focus for a new definition of conservation: (*i*) It emphasizes the economic aspects of biology and thus it fosters over-valuation of those natural entities that are of direct use to man; (*ii*) It ignores intrinsic values by discounting the complex interrelations between "useful" and "nonuseful" organisms that characterize ecosystem function; as Leopold (1949) noted, "One basic weakness in a conservation system based wholly on economic motives is that most members of the land community have no economic value" but they are "(as far as we know) essential to its healthy functioning"; (*iii*) Wise use is often seen as synonymous with multipurpose use or multiple use that "usually involves an interminable succession of piecemeal additions of new more intensive uses through time and a stepwise ecological shift away from the initial wild state" (Francis et al. 1979); and (*iv*) It signifies continued reliance on an anthropocentric philosophy which holds that "only people possess *intrinsic* value, while nature possesses merely *instrumental* value" (Callicott 1991).

Toward a conservation ethic and a definition

Neither the Romantic Preservation Ethic nor the Resource Conservation Ethic provides a viable foundation for a modern definition of conservation because both represent pre-ecological views of the environment. The first rejects scientific argument entirely, demanding specific, quasireligious commitments that are incompatible with the secular and multifaith societies of today. The second is rooted in a 19th century scientific paradigm that has been superseded by a deeper understanding of environmental realities (Callicott 1991). With its evolutionary and ecological basis, Callicott (1991) argues that Leopold's land ethic "ought to supplant its 19th century antecedents": it is less constrained by the cultural biases that taint the earlier views and it generates management policies that should be acceptable to moderates from both sides of the conservation movement. This ethical position leads to a definition of conservation that recognizes roles for both wise use and preservation but adopts neither as its central premise.

This definition can be developed within the context of current ecological knowledge. Odum (1959) saw conservation in the broadest sense as "probably the most important application of ecology" and he considered the principle of the ecosystem as "the basic and most important principle underlying conservation." Current science views the ecosystem as an integrated collection of abiotic and biotic entities that interact through exchanges of matter and energy (Allen and Hoekstra 1992; Pickett et al. 1992). A major theme is the continuity of ecosystem processes in the face of significant temporal variation in its abiotic components (Pickett et al. 1992). This ability to maintain functional continuity is essential to ecosystem sustainability and has been equated with such desirable qualities as ecosystem integrity and ecosystem health. Another major theme is the role of biodiversity in determining the degree of integration among system components and in supplying the functional redundancy necessary to ensure long-term system sustainability (Allen et al. 1993). In a conservation context, it is important to recognize the distinction between ecosystem function and ecosystem biodiversity. As Allen et al. (1993) pointed out, these two qualities should be treated separately because preservation of ecosystem function is a necessary, but not sufficient, condition to ensure preservation of biodiversity.

From this ecosystem perspective, conservation should mandate the safeguarding of healthy life-support systems that "are the ecological processes that keep the planet fit for life. They shape climate, cleanse air and water, regulate water flow, recycle essential elements, create and regenerate soil, and enable ecosystems to renew themselves" (World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991). In addition, conservation should mandate the control of major stresses (e.g., habitat alteration, exploitation, species introductions) to mitigate negative effects on ecosystem function and biodiversity. The goal of conservation should be healthy ecosystems. This goal is consistent with the land ethic. It can be achieved by ensuring that native biota are sustained in harmony with their natural environments. A conservation ethic based on ecological values requires that humans derive social, economic, recreational, and cultural benefits in a sustainable manner. A definition of conservation consistent with this position follows:

> the protection, maintenance, and rehabilitation of native biota, their habitats, and life-support systems to ensure ecosystem sustainability and biodiversity.

This definition of conservation does not contain the terms use or sustainable use. Conservation can no longer imply just use or advocate use as its central tenet. Conservation must clearly warrant the limitation of use to ensure ecosystem sustainability. In some situations, effective conservation will demand complete prohibition of use. This definition is sufficiently broadly based to include preservation through protection and use through maintenance (e.g., as in maintaining a vehicle that is being used by periodic servicing). We use the term rehabilitation to mean "to return a degraded ecosystem or population to an undegraded condition, which may be different from its original condition" (World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991).

The definition does not include the terms restoration ("to return a degraded ecosystem or population to its original condition") or enhancement ("increasing the capacity of an ecosystem or population to fulfil a particular function or yield a specified product") (World Conservation Union, United Nations Environment Programme, and World Wide Fund for Nature 1991) because (*i*) restoration may be difficult, if not impossible, to achieve in most cases (Francis et al. 1979; Meffe 1995) and (*ii*) attempts at rapid alteration of natural carrying capacities through enhancement activities such as the stocking of desirable exotic species weakens existing ecosystem structure and function (Evans et al. 1987). Community transformations via species invasions and deliberate stocking of exotics (vis à vis enhancement) also make recolonization attempts with native species more difficult (Evans and Olver 1995). Loftus (1976) recommended that rehabilitation should be the approach used in Canadian fisheries science; he rejected enhancement, arguing that it was quite a different approach and perhaps even antagonistic to rehabilitation.

This definition does not preclude the introduction of exotic species, nor does it require blanket acceptance of the consequences of unplanned invasions. However, experience has shown that exotic introductions often have unexpected, negative consequences for native ecosystems that are very difficult to reverse. Thus, we believe such introductions should be carefully evaluated to ensure protection of existing native biodiversity.

Conservation principles for fisheries management

Having offered a definition of conservation, and a rationale to justify it, we now consider how these ideas can be applied in a fisheries management context. Our objective is to develop a set of practical principles that will guide fisheries managers in their role of maintaining the viability

of living aquatic resources, and thus ensuring ecosystem sustainability.

Our definition focuses on overall objectives that are ecosystemic. However, typical conservation activities focus on populations of single species without direct reference to ecosystem consequences. This is partly because such populations are usually more obvious and easier to study than communities, landscapes, or genes (Noss 1990). As Magnuson (1976) noted, interactions between populations (e.g., predation and competition) form the heart of the functional aspects of community ecology. Without a reliable methodology that can be applied directly at the ecosystem level, population-based conservation may be the most practical way "to begin to cope with the issue of whole system viability" (Soulé 1987). Significant, but indirect, protection for the entire ecosystem may be provided by actions designed to preserve the viability of populations that fill key functional roles in the system. This approach, founded on such familiar concepts as keystone predators, indicator organisms, and integrator species may be the most effective way currently available to achieve ecosystem sustainability.

A population-level focus is particularly applicable to fisheries management because human exploitation of fish resources has traditionally focused on populations of particular species, which tend to be managed in isolation. What modern conservation ideas demand from management practice is explicit consideration of the ecosystem context that underlies the sustainability of any population (Andrewartha and Birch 1984). Classical practice treated an exploited population as an isolated entity, cut off from its past (i.e., its evolutionary history and consequent genetic heterogeneity), and independent of the abiotic and biotic components of its supporting ecosystem. Modern practice must explicitly recognize the essential roles that all of these components play in determining the sustainability of individual populations, and consequently of entire ecosystems.

The particular importance of genetic heterogeneity to management practice has been the focus of much recent work (Allendorf and Ryman 1987; Ryman and Utter 1987; Hindar et al. 1991). Such considerations, embodied under the rubric of the stock concept, now play a significant role in many fisheries management actions. Stocks are reproductively isolated subunits of populations that may, over time, become genetically differentiated. If the number of stocks involved in a fishery and their relative abundance is not known, the possibility of overfishing will always exist (see Loftus and Regier 1972, for examples drawn from North American Great Lakes fisheries). Even if stock composition is known, allowable harvests must be kept well below values considered as optimal given the history of fisheries exploitation (Larkin 1977; Peterman 1977; Ludwig et al. 1993). In the long term, population sustainability requires stock sustainability and thus stock-specific management. For all of the reasons outlined above, we have made fish stocks the primary focus of the principles espoused in this paper.

Fundamental principle

The primary goal of fisheries management is to ensure the perpetuation of self-sustaining stocks of indigenous aquatic species and, where possible, to allow their sustainable use. A commitment to resource maintenance is essential to preserve the biological base for such use. The principle can be stated as

- aquatic ecosystems should be managed to ensure long-term sustainability of native fish stocks.

Despite efforts to shift the focus of fishery management from species' stocks to multispecies assemblages, most fishery management practice is still stock oriented (Mercer 1982). In an evaluation of New Zealand's approaches to conservation, Towns and Williams (1993) argue that species-, or stock-, oriented approaches must be viewed as complementary to community- or guild-oriented and habitat-oriented approaches. Rich (1939) foresaw that conservation and rehabilitation of salmon (and we would argue other species), if it were to be successful, would have to occur at the stock level.

Thus, the key to conservation is sustainability of naturally reproducing wild stocks of native fish. These stocks embody thousands of years of evolutionary adaptations to local environments. The unique biological suitability of native stocks to their resident water bodies ensures that they are best able to withstand significant human use without serious deterioration in their long-term sustainability. These small, spatially isolated stocks are important guarantors of the genetic diversity of a species. In particular, stocks that occur in marginal habitats that may be active sites of natural selection may be of adaptive significance to the species as a whole (Scudder 1989; Northcote 1992).

The role of hatcheries and stocking in conservation must be re-evaluated. Hatchery programs intended to supplement existing wild, native stocks may have the opposite effect. The artificial selection process in hatcheries favours domestic, as opposed to wild, traits. Subsequent inbreeding with wild stocks can quickly undo thousands of years of natural selection and lead to loss of local stocks (Nehlsen et al. 1991; Hilborn 1992). Recruitment overfishing of wild stocks, stimulated by the planting of hatchery fish, can have the same effect (Evans and Willox 1991). The stocking of hatchery fish to mitigate stock declines, caused primarily by other factors such as habitat degradation and dam construction, can also accelerate the loss of wild stocks (Nehlsen et al. 1991), while failing to address the primary causes of population decline. The overall effect is a loss of genetic diversity. The reliance on technological solutions such as the stocking of hatchery fish to redress man-made problems has been at the expense of ethical, ecological, and genetic considerations (Scarnecchia 1988; Hilborn 1992; Meffe 1992). Meffe (1992) has called this "techno-arrogance," an attitude that has clearly undermined conservation efforts. Artificial fisheries, which rely wholly on stocking for their continued existence, are not sustainable and thus have no part in a conservation ethic.

Even while the inadequacies of fisheries management strategies based on hatcheries and stocking are becoming evident, investments in intensive aquaculture are growing rapidly. Aquaculture is not based on conservation principles and, when practiced in natural systems, it may enhance

the degradation and abandonment of sustainable fisheries. In such systems, aquaculture can contribute to the genetic deterioration and loss of natural stocks, enhance the spread of diseases, accelerate the rates of invasion of exotic species, and promote habitat destruction and degradation (Folke et al. 1994).

Stocks are the repository of the genetic diversity within each species and are the building blocks on which fisheries management is based. Hence, the focus on fish stocks in the development of conservation principles is appropriate. Species and, by extension, stock diversity is a reliable indicator of biodiversity in aquatic systems (Moyle and Leidy 1992). Thus, a focus on preserving fish stock diversity is a practicable strategy for protecting overall biodiversity of aquatic systems. As fish are often primary determinants of ecosystem structure (Brooks and Dodson 1965; McQueen et al. 1986; Carpenter 1988), protecting extant fish assemblages should usually protect extant ecosystem structure. In an individual water body, a population may be composed of one or several stocks. We believe that primary conservation requirements are met when the sustainability of individual fish stocks is secured.

Supporting principles

To ensure ecosystem protection, degradation of the physical environment (e.g., habitat destruction), the chemical environment (e.g., water quality deterioration), and the biological environment (e.g., transfer of non-native stocks, introduction of exotic species) should be prevented. To ensure sustainable use of fish stocks, those populations that can be exploited, and those that cannot, need to be identified. For populations that can be exploited, the amount of harvest must be limited and the manner of harvesting must be controlled. The principles that we believe are necessary to effectively guide such actions are outlined below.

Principles of ecosystem protection

- The sustainability of a fish stock requires protection of the specific physical and chemical habitats utilized by the individual members of that stock.

The existence of clean, undamaged environments is critical to sustainability. The biological processes that underlie sustainability require good substrate, adequate water supply, suitable thermal characteristics, and good water quality. Habitat alterations or modifications that decrease ecological productivity will undermine efforts to conserve stocks. The right to use ecological productivity does not bestow the right to abuse it. Attempts to conserve habitat often depend on simplified assumptions that (*i*) the level of productivity is roughly proportional to the supply of suitable habitat and (*ii*) the loss of habitat units that are noncritical will not noticeably affect sustainable levels of the preferred use, exploitation. Recent research by Pulliam and Danielson (1991) challenges these simple models. Good habitats may facilitate surplus production but other, mediocre or poor, habitats may be necessary to accommodate the accumulated biomass. Hence, the total habitat may be required to support the level of biomass needed to support harvest expectations. Preserving critical spawning habitats may be pointless if there is nowhere for adults to live before becoming vulnerable to exploitation. In related studies, Danielson (1991, 1992) has shown how changes in the relative supplies of different habitat types can shape the outcome of interspecific interactions. Sutherland and Anderson (1993) showed, with simple models, how biased elimination of better or poorer habitat units in a fragmented landscape can determine the shape of the relationship between sustainable population size and overall habitat supply.

Given the temptation to measure the degree of conservation success within fisheries in terms of productivity or potential yield, there is a clear danger that ecosystem modifications that increase production, such as climate warming, eutrophication, or aquaculture, might be viewed as changes that are consistent with conservation objectives. However, if the prior, undegraded condition of an ecosystem provides the direction for rehabilitation efforts and the benchmark for achievement of sustainable conservation success, any action that moves an ecosystem away from that benchmark state may be clearly judged as degradation.

- The sustainability of a fish stock requires maintenance of its supporting native community.

Degradation of the biological environment, via the transfer of non-native stocks and the introduction of exotic species, must be prevented. Transfers of non-native organisms inevitably result in the loss of locally adapted gene pools. In the Great Lakes basin, the invasion of species like sea lamprey, *Petromyzon marinus*, alewife, *Alosa pseudoharengus*, and rainbow smelt, *Osmerus mordax*, and the introduction of species like common carp, *Cyprinus carpio*, have had considerable, negative impacts on native fish communities (Emery 1985; Crossman 1991).

Hence, deliberately adding species to increase species richness, or more likely to improve exploitation opportunities, cannot be considered a conservation action. The consequent alteration to the productivity of natural ecosystems and the loss of surplus production from native stocks undermines sustainability. In addition, the accompanying degradation of biological habitats represents an irreversible shrinkage in the reservoir of biodiversity that uniquely characterizes each region of Canada.

The rates of deliberate introductions and accidental, but usually man-assisted, invasions are continuing to increase (Crossman 1991; Welcomme 1992; Carlton and Geller 1993). The history of introductions of organisms foreign to native ecosystems is replete with examples demonstrating severe, detrimental effects (Billington and Hebert 1991; Mills et al. 1991). Managing with exotics has been compared to a game of chance (Magnuson 1976), where positive results cannot be guaranteed (Regier 1968). Because changes wrought by such introductions can be extreme and because net results are hard to predict, proposed introductions should be forbidden, unless a situation-specific evaluation confirms that the risk to existing ecosystems is minor. Invasions present a more complex problem, although species transfers by ships' ballast water, the major

route in the North American Great Lakes, are now receiving more urgent attention (Carlton and Geller 1993). Carlton and Geller (1993) have characterized these exotic additions as a form of ecological roulette.

Principles of population utilization

- Vulnerable, threatened, and endangered species must be rigidly protected from all anthropogenic stresses.

By definition, the stocks of such species face various degrees of risk of extinction. Removal and (or) prevention of anthropogenic stresses would significantly reduce this risk.

These organisms are irreplaceable segments of the heritage of biodiversity that uniquely characterizes the biota of a region. Any activity that risks their extinction should be proscribed. In Canada, the selection of species at risk and their classification is decided by the Committee on the Status of Endangered Wildlife in Canada, which comprises representatives from federal, provincial, and private agencies. In April, 1993, 35 wild species, subspecies, or separate populations of fish were designated as vulnerable, 11 as threatened, and 3 as endangered (Committee on the Status of Endangered Wildlife in Canada 1993). However, the determinations of the committee have no legal status so that each jurisdiction must provide its own appropriate safeguards to risks imposed on these designated species, subspecies, or separate populations.

- Exploitation of populations or stocks undergoing rehabilitation will delay, and may preclude, full rehabilitation.

For stocks undergoing rehabilitation, any exploitation will delay full rehabilitation and increase the risk of failure. If some harvesting occurs, it should be strictly controlled to ensure that mortality rates do not prevent rehabilitation and are, in fact, low enough to let rehabilitation proceed at a reasonable rate. Allowing higher mortality rates will ensure the perpetuation of put-and-take hatchery-dependent fisheries that may masquerade as rehabilitation projects. If harvest for other species is allowed, fishing practices should minimize the capture of the stock undergoing rehabilitation. This is difficult to achieve in mixed stock fisheries, which should be managed for the protection of the least sustainable individual stock within the mix, or a more selective means of harvesting individual stocks should be found.

- Harvest must not exceed the regeneration rate of a population or its individual stocks.

Exploitation can only be sustained if it is restricted to the annual generation of fish protein that exceeds the maintenance requirements of a population, or its individual stocks. Extinction is inevitable if losses exceed the natural capacity of a population to replenish itself. This is a common characteristic of all renewable resources: sustainable use is equivalent to renewal rate (Daily and Ehrlich 1992). Similar behaviour is well known in economics (Costanza and Daly 1992): exhaustion of capital will occur if annual expenditures exceed interest income. Planned harvest rates should also be sensitive to other uses and stresses imposed on the stock and other ecosystem components. They should acknowledge natural temporal variation in the productivity of the target population and of the ecosystem of which it is a part.

In natural populations, annual regeneration rates vary widely from year to year and cannot be accurately predicted. Given the amplitude of such natural variation, population sustainability can only be guaranteed if fisheries are managed in a cautious manner. Ludwig et al. (1993) offer some sombre reflections on the difficulties of achieving sustainability of exploited fisheries resources. To provide a sufficient margin of safety, total allowable catch should be set well below maximum annual regeneration rates. A variety of formulae have been developed in fisheries science with the aim of establishing defensible limits on exploitation: MSY, OY, $F_{0.1}$, etc. (Parsons 1993). Mostly, these approaches have been developed for single-species stocks, ignoring the ecosystem contexts in which they exist. Some methods developed for multispecies assemblages take account of energy flow dynamics and species interactions. Stock exploitation limits that recognize intrinsic ecosystem dynamics are likely to be more stringent than those obtained by assessing each species in isolation.

The need for caution in exploiting long-lived species is paramount. Such species typically are slow growing, are late maturing, have a low reproductive potential, and have a low turnover or regeneration rate. They may spawn infrequently. Consequently, they require multiple opportunities to spawn and recruit offspring and long recovery times when populations are depressed. For such species, protection of adults is absolutely critical to long-term population stability. The need to exercise caution may be especially critical for long-lived species that are terminal in the food chain because they exert a dominant role in the integration and maintenance of community structure (Evans et al. 1987; Johnson 1994). Pauly et al. (1989) referred to the decline of fisheries for such key species as ecosystem overfishing.

- Direct exploitation of spawning aggregations increases the risk to sustainability of fish stocks.

Stock sustainability requires that the number of adult fish escaping harvest (i.e., spawner escapement) be sufficient to maintain the reproductive output of the stock. As spawner escapement drops toward zero, the risk to stock sustainability increases rapidly.

The impact of a fixed harvest on spawner escapement is minimized if harvested fish are taken at random from the stock and is maximized if harvested fish are taken directly from aggregations of spawning adults. For example, consider a quota of 10 000 fish applied to a stock containing 40 000 fish big enough to satisfy fishers, of which 10 000 fish are big enough to spawn. If the quota is taken at random from the stock, the number of spawners will be

reduced about 25%. If the quota is taken from spawner aggregations, all spawners will be removed and the stock will be threatened with extinction. The risk to sustainability (measured in terms of potential reductions in spawner abundance) imposed by spawner targeting can only be ameliorated by significant reductions in allowable harvest. In our simple example, a 75% reduction in harvest would be required to lower the risk imposed by spawner targeting to that imposed by random selection.

Thus, when spawners are targeted for exploitation, conservation needs demand relatively low harvest levels and strict harvest monitoring to keep the risk to stock sustainability at an acceptable level. This requires information-intensive management (i.e., accurate monitoring of both stock abundance and harvest), which is extremely expensive, and thus justifiable only for those stocks that support large, economically important fisheries. Many oceanic stocks fall into this category (e.g., the cod stocks of the east coast of Canada and the anadromous stocks of the west coast of Canada). However, recent experience (e.g., Finlayson 1994, on the demise of northern stocks of the Atlantic cod (*Gadus morhua*)) suggests that the environments inhabited by such stocks are so vast and complex that it is extremely difficult to get the precise information needed to micromanage spawner-targeted fisheries effectively, even when large amounts of money are set aside to acquire that information. As Hilborn et al. (1993) point out, uncertainty in stock assessment and risk in decision making cannot be eliminated, although both can and must be dealt with.

The west coast anadromous stocks spend much of their life cycle in oceanic habitats so large that efficient harvesting is not possible. Only when they form natural aggregations, just before spawning, are they sufficiently concentrated in space to be effectively harvested. The abundance and economic value of these stocks justify large expenditures for the assessment and enforcement activities necessary to restrict spawner-targeted harvests to levels where the risk to sustainability is acceptable. However, despite large current expenditures on such activities, many stocks are in decline (Nehlsen et al. 1991; Waples 1991; Hilborn and Winton 1993), thus suggesting that effective micromanagement of these stocks may also cost far more than is currently appreciated.

Among freshwater species, only a tiny percentage of the millions of discrete stocks scattered throughout the lakes and rivers of Canada are of sufficient economic importance to support the information-intensive, micromanagement practices demanded by spawner-targeted harvesting. To subject such stocks to spawner-targeted harvesting, without escapement monitoring and absolute abundance estimates, would expose the sustainability of these stocks to risks that are both avoidable and unnecessary. In the vast majority of cases, the efficiency of modern fishing gear is high enough, and dispersal of individuals low enough, to permit cost-effective harvesting of these populations without targeting spawning aggregations.

Harvest theory points to the avoidable damage that spawner targeting can inflict on stock sustainability. In principle, this damage is reversible: a harvest moratorium or harvest refuge (sensu Carr and Reed 1993) may allow regeneration of a depleted stock. However, genetic considerations point to long-term damage that is irreversible (Soulé 1987). When spawners are targeted, exploitation is focused on the only natural measure of stock success, reproduction: only those fish that survive to maturity and are successful in reaching the spawning grounds are killed. By imposing direct selection against successful reproduction, deleterious changes in the population gene pool are likely. Among species that home to specific breeding sites, selection will act against homing and imprinting abilities. Selection will also act against those genetic subgroups that use the exploited spawning sites, leading eventually to elimination of those groups from the population. Among species that have specific spawning periods, selection will act to narrow the range of spawning times, typically favouring spawning times that are later than normal. All such changes reduce the ability of a stock to maintain itself in its natural environment and thus damage stock sustainability.

Additional negative effects that accompany spawner targeting include (*i*) increased risk of inadvertently exceeding allowable harvest; increased risk stems from increased vulnerability of spawning fish to capture: use of killing gear (e.g., gill nets) exacerbates the problem because excess harvest cannot be released alive; and (*ii*) habitat damage and disruption of reproductive behaviour: spawning habitat may be damaged by the placement and use of fishing gear; activity accompanying placement and use of gear may also disrupt the reproductive behaviour of the fish themselves; both effects violate the principle of habitat protection.

The potential for undermining population sustainability by targeting adults during their reproductive periods is well recognized in conservation genetics (Lande and Barrowclough 1987; Soulé 1987). Experience in freshwater systems has shown that one of the most cost-effective ways to control nuisance or invading species is to focus intense exploitation on their spawning aggregations. Small, discrete spawning stocks are particularly vulnerable to elimination caused by intense spawner exploitation and genetic deterioration caused by moderate spawner exploitation. Yet, stocks of this sort are important contributors to the genetic diversity of individual populations and to the biodiversity of the species as a whole.

From the arguments presented above, it is clear that, at any level of exploitation, the targeting of spawning fish imposes an additional risk to population sustainability. While the risk may be partly ameliorated by quantitative monitoring of stock abundance and harvest, this is usually practicable only for large populations with known stock compositions. Such populations would have spawner abundances ranging from several thousand to hundreds of thousands of fish, and would include many oceanic, anadromous species where the economic and social value of the fisheries justifies the cost of information-intensive management.

For smaller populations, with unknown stock compositions, such intensive management will rarely be practicable and, where practicable, may not be particularly effective because smaller populations are inherently less predictable than larger populations (Weinberg 1975, p. 20). Such

populations would have spawner abundances ranging from less than 100 to several thousand individuals and would include most of the freshwater stocks in Canada's inland lakes and rivers. Generally, spawner-targeted harvesting of such stocks would impose a risk to their sustainability high enough to violate conservation requirements.

The application of conservation principles

At the federal level in Canada, two documents guide the management of fishery resources: the Fisheries Act of 1967 with subsequent revisions, and the Policy for the Management of Fish Habitat issued in 1986 (Department of Fisheries and Oceans 1986). The Act imposes the goal of conservation and protection while the Policy aims for no net loss of productive capacity of fish habitats. In some provinces, relevant policy documents have been developed that are compatible with federal objectives. For example, the policy documents produced by the Ontario Ministry of Natural Resources, Direction '90s (Ontario Ministry of Natural Resources 1991) and the Strategic Plan for Ontario Fisheries, known as SPOF II (Ontario Ministry of Natural Resources 1992), embrace an ecosystem approach to managing fisheries.

At a more prosaic level, the application of conservation principles in the daily work routine of most fisheries biologists relates to determinations they make about resource extraction and development issues. This usually requires them to develop guidelines or regulations to control harvest and protect habitat. The natural tendency to provide oversimplified operational definitions of conservation should be resisted. For example, adequate local control of exploitation cannot be strictly based on species-specific, provincial fecundity and productivity standards. Such standards, while useful first approximations, ignore, of necessity, local circumstances (see Ontario Ministry of Natural Resources 1982 for an example of how a knowledge of local conditions can be used to modify provincial yield guidelines). Without this type of evaluation, the standards sanction harvest levels that approach short-term maximum extraction rates. Such levels are clearly not sustainable because they afford a low margin of safety and take no account of temporal and spatial variation in reproductive success.

The primary literature contains a variety of methods for estimating the optimal sustained yield for individual fish populations in a water body. These studies also discuss why harvests in local waters may vary considerably from predicted values and how yield estimates can be adjusted to provide a closer match to local conditions. Such estimates do provide useful reference points for establishing the lower harvest necessary to provide the margin of safety required to protect stock sustainability. These adjustments require specific knowledge of the water bodies involved and the manner of harvesting. For example, allowable yield should be lower when spawners are targeted for harvest.

Sanctuaries and harvest refuges can be effective tools for applying conservation principles to management issues, particularly those involving immediate threats to stock sustainability. Sanctuaries are water bodies, or parts thereof, where removal of any fish species is prohibited, either for a short period to provide protection to spawning aggregations or for much longer times to allow for rehabilitation of fish stocks. Using examples from coastal marine fisheries and reef fishes in particular, Carr and Reed (1993) define harvest refuges as areas where harvest of target species is restricted, and where the intent of rebuilding stocks of such species is through larval recruitment. It is not clear to us whether the authors include prohibition within the meaning of restriction. Local circumstances, however, will surely dictate a large variety of harvest control regimes including no fishing of target species in some refuges, although fishing for other species may or may not be allowed. Regardless of the type or degree of protection, sanctuary or refuge status should be withdrawn only when special protection is no longer required.

Routine monitoring of ecosystem status is critical to measuring or understanding the status of conservation efforts. For those resources that undergo harvest, stocks must be assessed occasionally, harvest must be determined periodically as a check against sustainable levels, and compliance must be assured. Stock assessment is expensive, but we see no alternative to a judicious and modest program of routine monitoring.

Our intent in presenting this perspective on conservation, vis à vis fish and fisheries, is twofold: to promote an ecological ethic as the foundation for developing a set of conservation principles for the management of fisheries resources in Canada, and to present a set of conservation principles for fisheries management that will evoke a debate about just what those principles ought to be. With respect to the former, we would expect general support from the fisheries community, but we are under no illusion that the fisheries community will endorse this preliminary statement of conservation principles. Any subsequent debate that this article may spark will, however, contribute to a further refinement and elucidation of such principles. This can only benefit the resource, its stewards, and its users.

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References

Allen, T.F.H., and T.W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York. 384 p.

Allen, T.F.H., B.L. Bandurski, and A.W. King. 1993. The ecosystem approach: theory and ecosystem integrity. Report to the Great Lakes Science Advisory Board, International Joint Commission, Windsor, Ont. 64 p.

Allendorf, F.W., and N. Ryman, 1987. Genetic management of hatchery stocks, p. 141–159. *In* N. Ryman and F. Utter [ed.] Population genetics and fishery management. University of Washington Press, Seattle, Wash. 420 p.

Andrewartha, H.G., and L.C. Birch. 1984. The ecological web. Cambridge University Press, Cambridge, England. 506 p.

Baumer, F.L. 1973. Romanticism, p. 198–204. *In* P. Weiner [ed.] Dictionary of the history of ideas. Charles Scribner, New York. 485 p.

Billington, N., and P.D.N. Hebert [Eds]. 1991. International symposium on the ecological and genetic implications of fish introductions. Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 1–181.

Boas, G. 1973. Nature, p. 346–351. *In* P. Weiner [ed.] Dictionary of the history of ideas. Charles Scribner, New York. 485 p.

Brooks, J.L., and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science (Washington, D.C.), 150: 28–35.

Callicott, J.B. 1991. Conservation ethics and fishery management. Fisheries, 16: 22–28.

Carlton, J.T., and J.B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science (Washington, D.C.), 261: 78–82.

Carpenter, S.R. 1988. Complex interactions in lake communities. Springer-Verlag, New York. 283 p.

Carr, M.H., and D.C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. Can. J. Fish. Aquat. Sci. 50: 2019–2028.

Christie, W.J., M. Becker, J.W. Cowden, and J.R. Vallentyne. 1986. Managing the Great Lakes as a home. J. Gt. Lakes Res. 12: 2–17.

Clarke, C.H.D. 1963. A philosophy of conservation, p. 187–198. *In* J.R. Dymond [ed.] Fish and wildlife a memorial to W.J.K. Harkness. Longmans, Toronto. 214 p.

Committee on the Status of Endangered Wildlife in Canada. Canadian species at risk April 1993. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont. Ms Rep. 11 p.

Costanza, R., and H.E. Daly. 1992. Natural capital and sustainable development. Conserv. Biol. 6: 37–46.

Coventry, A.F. 1963. The naturalist in modern society, p. 17–27. *In* J.R. Dymond [ed.] Fish and wildlife a memorial to W.J.K. Harkness. Longmans, Toronto. 214 p.

Crossman, E.J. 1991. Introduced freshwater fishes: a review of the North American perspective with emphasis on Canada. Can. J. Fish. Aquat. Sci. 48(Suppl.1): 46–57.

Daily, G.C., and P.R. Ehrlich. 1992. Population, sustainability, and earth's carrying capacity. BioScience, 42: 761–771.

Danielson, B.J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. Am. Nat. 138: 1105–1120.

Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. Evol. Ecol. 6: 399–411.

Department of Fisheries and Oceans. 1986. Policy for the management of fish habitat. Fish Habitat Management Branch, Department of Fisheries and Oceans, Ottawa, Ont. 30 p.

Emery, L. 1985. Review of fish species introduced into the Great Lakes, 1819–1974. Gt. Lakes Fish. Comm. Tech. Rep. No. 45. 31 p.

Evans, D.O., and C.H. Olver. 1995. Introduction of lake trout, *Salvelinus namaycush*, to inland lakes of Ontario, Canada: factors contributing to successful colonization. J. Gt. Lakes Res. 21(Suppl. 1): 30–53.

Evans, D.O., and C.C. Willox. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 134–147.

Evans, D.O., B.A. Henderson, N.J. Bax, T.R. Marshall, R.T. Oglesby, and W.J. Christie. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. Can. J. Fish. Aquat. Sci. 44(Suppl. 2): 448–470.

Finlayson, A.C. 1994. Fishing for truth. Institute for Social and Economic Research, Memorial University of Newfoundland, St John's, Nfld. 176 p.

Folke, C., N. Kautsky, and M. Troell. 1994. The costs of eutrophication from salmon farming: implications for policy. J. Environ. Manage. 40: 173–182.

Francis, G.R., J.J. Magnuson, H.A. Regier, and D.R. Talhelm. 1979. Rehabilitating Great Lakes ecosystems. Gt. Lakes Fish. Comm. Tech. Rep. No. 37. 99 p.

Hays, S.P. 1959. Conservation and the gospel of efficiency. The progressive conservation movement, 1890–1920. Harvard University Press, Cambridge, Mass. 297 p.

Hewitt, C.G. 1918. Report of the Ninth Annual Meeting of the Commission of Conservation of Canada, Ottawa. 282 p.

Hilborn, R. 1992. Hatcheries and the future of salmon in the Northwest. Fisheries, 17: 5–8.

Hilborn R., and J. Winton. 1993. Learning to enhance salmon production: lessons from the Salmonid Enhancement Program. Can. J. Fish. Aquat. Sci. 50: 2043–2056.

Hilborn, R., E.K. Pikitch, and R.C. Francis. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.

Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural fish populations. Can. J. Fish. Aquat. Sci. 48: 945–957.

International Union for Conservation of Nature and Natural Resources. 1980. World conservation strategy. Living resource conservation for sustainable development. Prepared with the advice, cooperation, and financial assistance of the United Nations Environment Programme and the World Wildlife Fund and in collaboration with the Food and Agriculture Organization of the United Nations and the United Nations Educational, Scientific and Cultural Organization. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Johnson, L. 1994. Long-term experiments on the stability of two fish populations in previously unexploited arctic lakes. Can. J. Fish. Aquat. Sci. 51: 209–225.

Krakauer, J. 1991. Brownfellas. Outside, 16: 69–72, 114–116.

Lande, R., and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management, p. 87–123. *In* M.E. Soulé [ed.] Viable populations for conservation. Cambridge University Press, Cambridge, England. 189 p.

Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. Trans. Am. Fish. Soc. 78: 1–11.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York. 481 p.

Leopold, A. 1939. A biotic view of land. J. For. 37: 727–730.

Leopold, A. 1949. A Sand County almanac and sketches here and there. Oxford University Press, New York. 226 p.

Loftus, K.H. 1976. Science for Canada's fisheries rehabilitation needs. J. Fish. Res. Board Can. 33: 1822–1857.

Loftus, K.H., and H.A. Regier [Eds]. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation—lessons from history. Science (Washington, D.C.), 260: 17, 36.

Magnuson, J.J. 1976. Managing with exotics: a game of chance. Trans. Am. Fish. Soc. 105: 1–9.

McQueen, D.J., J.R. Post, and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571–1581.

Meffe, G.K. 1992. Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. Conserv. Biol. 6: 350–354.

Meffe, G.K. 1995. Genetic and ecological guidelines for species reintroduction programs: application to Great Lakes fishes. J. Gt. Lakes Res. 21(Suppl. 1): 3–9.

Mercer, M.C. [Ed]. 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59: 169 p.

Miller, A. 1986. The Delphi approach to the mediation of environmental disputes. Environ. Manage. 10: 321–330.

Mills, E.D., J.H. Leach, J.T. Carlton, and C.L. Secor. 1991. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. Gt. Lakes Fish. Comm. Res. Compl. Rep. 117 p.

Moyle, P.B., and R.A. Leidy. 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas, p. 127–169. *In* P.L. Fiedler and S.K. Jain [eds.] Conservation biology. Chapman and Hall, New York and London. 507 p.

Nash, R. 1969. Wilderness and the American mind. Yale University Press, New Haven, Conn. 256 p.

Nehlsen, W., J.E. Williams, and J.A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries, 16: 4–21.

Northcote, T.G. 1992. Migration and residency in stream salmonids: some ecological considerations and evolutionary consequences. Nord. J. Freshwater Res. 67: 5–17.

Norton, B.G. 1991. Toward unity among environmentalists. Oxford University Press, New York. 289 p.

Noss, R.F. 1990. Ideas for monitoring biodiversity: a hierarchical approach. Conserv. Biol. 4: 355–364.

Odum, E.P. 1959. Fundamentals of ecology. 2nd ed. W.B. Saunders Co., Philadelphia, Pa. 546 p.

Ontario Ministry of Natural Resources. 1982. Partitioning yields estimated from the morphoedaphic index into individual species yields. Report of SPOF Working Group No. 12. Ontario Ministry of Natural Resources, Toronto, Ont. 71 p.

Ontario Ministry of Natural Resources. 1991. Direction '90s. Ontario Ministry of Natural Resources, Toronto, Ont. 14 p.

Ontario Ministry of Natural Resources. 1992. Strategic plan for Ontario fisheries (SPOF II): an aquatic ecosystem approach to managing fisheries. Fisheries Policy Branch, Ontario Ministry of Natural Resources, Toronto, Ont. 22 p.

Parsons, L.S. 1993. Management of marine fisheries in Canada. Can. Bull. Fish. Aquat. Sci. 225: 763 p.

Pauly, D., G. Silvestre, and I.R. Smith. 1989. On development, fisheries and dynamite: a brief review of tropical fisheries management. Nat. Resour. Model, 3: 307–329.

Pepper, D. 1984. The roots of modern environmentalism. Croom Helm, London. 246 p.

Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. J. Fish. Res. Board Can. 34: 1130–1142.

Pickett, S.T.A., V.T. Parker, and P.L. Fiedler. 1992. The new paradigm in ecology: implications for conservation biology above the species level, p. 66–88. *In* P.L. Fiedler and S.K. Jain [eds.] Conservation biology. Chapman and Hall, New York and London. 507 p.

Pimm S.L. 1991. The balance of nature? University of Chicago Press, Chicago, Ill. 434 p.

Pinchot, G. 1947. Breaking new ground. University of Washington Press Americana Library edition 1972. University of Washington Press, Seattle, Wash. 522 p.

Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am. Nat. 137: S50–S66.

Regier, H.A. 1968. The potential misuse of exotic species as introductions, p. 92–111. *In* K.H. Loftus [ed.] A symposium on introductions of exotic species. Res. Rep. No. 82. Ontario Department of Lands and Forests, Research Branch, Toronto, Ont. 111 p.

Regier, H.A. 1976. Science for the scattered fisheries of the Canadian interior. J. Fish. Res. Board Can. 33: 1213–1232.

Regier, H.A., and E.A. Bronson. 1992. New perspectives on sustainable development and barriers to relevant information. Environ. Monit. Assess. 20: 111–120.

Regina versus Sparrow. 1990. Supreme Court Report. Vol. 1. p. 1075.

Rich, W.H. 1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. Contrib. No. 1. Fisheries Commission of Oregon, Portland, Oreg.

Ryman, N., and F. Utter [Eds]. 1987. Population genetics and fishery management. University of Washington Press, Seattle, Wash. 420 p.

Scarnecchia, D.L. 1988. Salmon management and the search for values. Can. J. Fish. Aquat. Sci. 45: 2042–2050.

Scudder, G.G.E. 1989. The adaptive significance of marginal populations: a general perspective, p. 180–185. *In* C.D. Levings, L.B. Holtby, and M.A. Henderson [eds.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. No. 105.

Sifton, C. 1910. Report of the First Annual Meeting of the Commission of Conservation of Canada. Mortimer, Ottawa. 216 p.

Soulé, M.E. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, England. 189 p.

Sutherland, W.J., and C.W. Anderson. 1993. Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. J. Theor. Biol. 160: 223–230.

Towns, D.R., and M. Williams. 1993. Single species conservation in New Zealand: towards a redefined conceptual approach. J. R. Soc. N.Z. 23: 61–78.

Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 124–133.

Weinberg, G.M. 1975. An introduction to general systems thinking. John Wiley and Sons, New York. 279 p.

Welcomme, R.L. 1992. A history of international introduction of inland aquatic species. ICES Mar. Sci. Symp. 194: 3–14.

World Commission on Environment and Development. 1987. Our common future. Oxford University Press, Oxford, England. 400 p.

World Conservation Union, United Nations Environment Programme, and World Wide Fund For Nature. 1991. Caring for the earth. A strategy for sustainable living. Published in partnership by the World Conservation Union, the United Nations Environment Programme, and the World Wide Fund For Nature, Gland, Switzerland. 228 p.

Erratum: Phylogenic relationships among Palearctic and Nearctic whitefish (*Coregonus* sp.) populations as revealed by mtDNA variation

Louis Bernatchez and Julian J. Dodson

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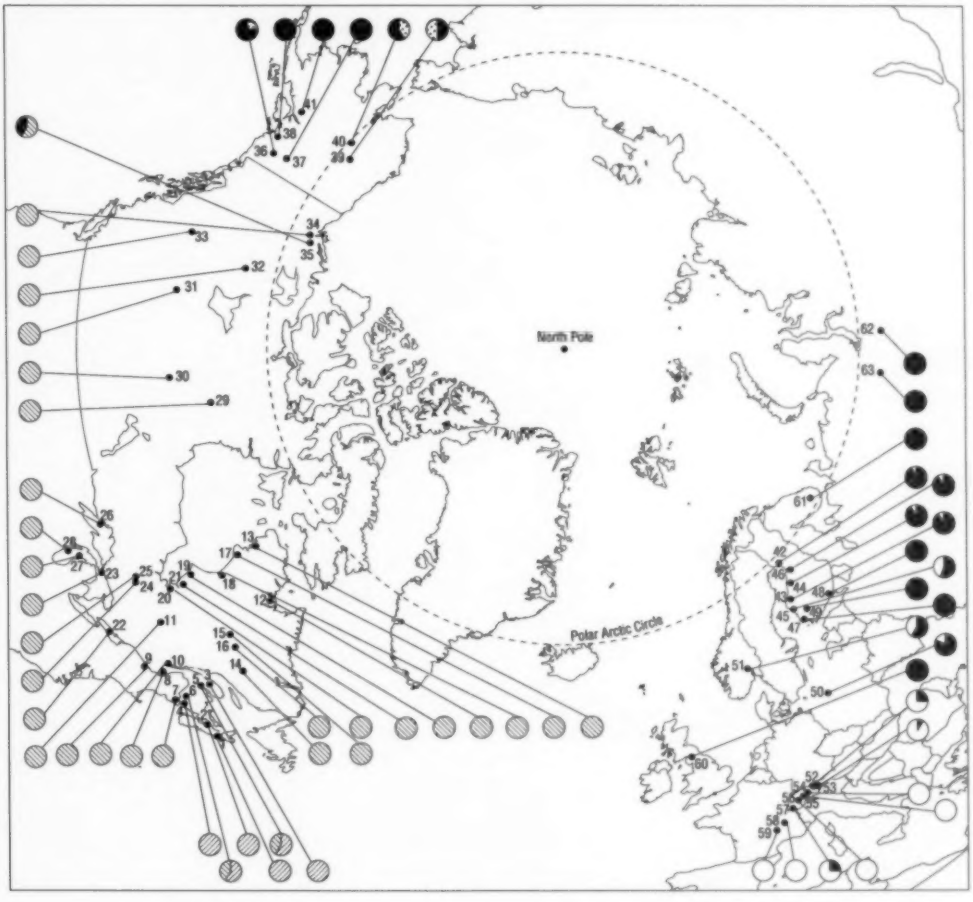

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Contents (concluded) / Table des matières (suite et fin)

John M. Emlen	**1442–1448**	Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*)
A. Ricciardi, F.G. Whoriskey, and J.B. Rasmussen	**1449–1461**	Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density
Nicholas E. Mandrak	**1462–1474**	Biogeographic patterns of fish species richness in Ontario lakes in relation to historical and environmental factors
P. Pepin, J.A. Helbig, R. Laprise, E. Colbourne, and T.H. Shears	**1475–1486**	Variations in the contribution of transport to changes in planktonic animal abundance: a study of the flux of fish larvae in Conception Bay, Newfoundland
Brian M. Wood and Mark B. Bain	**1487–1498**	Morphology and microhabitat use in stream fish
Charles K. Minns	**1499–1508**	Allometry of home range size in lake and river fishes
Ora E. Johannsson	**1509–1522**	Response of *Mysis relicta* population dynamics and productivity to spatial and seasonal gradients in Lake Ontario
Carl Walters	**1523–1534**	Estimation of historical stock sizes and recruitment anomalies from relative abundance time series
Kim N.I. Bell, Pierre Pepin, and Joseph A. Brown	**1535–1545**	Seasonal, inverse cycling of length- and age-at-recruitment in the diadromous gobies *Sicydium punctatum* and *Sicydium antillarum* in Dominica, West Indies
Peter S. Rand, Donald J. Stewart, Brian F. Lantry, Lars G. Rudstam, Ora E, Johannsson, Andrew P. Goyke, Stephen B. Brandt, Robert O'Gorman, and Gary W. Eck	**1546–1563**	Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario
Lisa A. Eby, Lars G. Rudstam, and James F. Kitchell	**1564–1571**	Predator response to prey population dynamics: an empirical analysis based on lake trout growth rates
Doran M. Mason, Andrew Goyke, and Stephen B. Brandt	**1572–1583**	A spatially explicit bioenergetics measure of habitat quality for adult salmonines: Comparison between Lakes Michigan and Ontario
		PERSPECTIVE
C.H. Olver, B.J. Shuter, and C.K. Minns	**1584–1594**	Toward a definition of conservation principles for fisheries management
		ERRATUM
Louis Bernatchez and Julian J. Dodson	**1595**	Erratum: Phylogenic relationships among Palearctic and Nearctic whitefish (*Coregonus* sp.) populations as revealed by mtDNA variation

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ARTICLES

M.R. van den Heuvel, K.R. Munkittrick, G.J. Van Der Kraak, M.R. Servos, and D.G. Dixon	**1339–1350**	Hepatic 7-ethoxyresorufin-*O*-deethylase activity, plasma steroid hormone concentrations, and liver bioassay-derived 2,3,7,8,-TCDD toxic equivalent concentrations in wild white sucker (*Catostomus commersoni*) caged in bleached kraft pulp mill effluent
G.A. De Leo and M. Gatto	**1351–1367**	A size and age-structured model of the European eel (*Anguilla anguilla* L.)
You-Gan Wang and Mervyn R. Thomas	**1368–1375**	Accounting for individual variability in the von Bertalanffy growth model
Robert H. Devlin, Timothy Y. Yesaki, Edward M. Donaldson, Shao Jun Du, and Choy-Leong Hew	**1376–1384**	Production of germline transgenic Pacific salmonids with dramatically increased growth performance
S. Gudjonsson, S.M. Einarsson, Th. Antonsson, and G. Gudbergsson	**1385–1398**	Relation of grilse to salmon ratio to environmental changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland
John M. Kalish	**1399–1405**	Application of the bomb radiocarbon chronometer to the validation of redfish *Centroberyx affinis* age
R.A. Reid, K.M. Somers, and S.M. David	**1406–1420**	Spatial and temporal variation in littoral-zone benthic invertebrates from three south-central Ontario lakes
Anthony J. Fowler, Steven E. Campana, Cynthia M. Jones, and Simon R. Thorrold	**1421–1430**	Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using solution-based ICPMS
Anthony J. Fowler, Steven E. Campana, Cynthia M. Jones, and Simon R. Thorrold	**1431–1441**	Experimental assessment of the effect of temperature and salinity on elemental composition of otoliths using laser ablation ICPMS

Continued on inside back cover / Suite au verso

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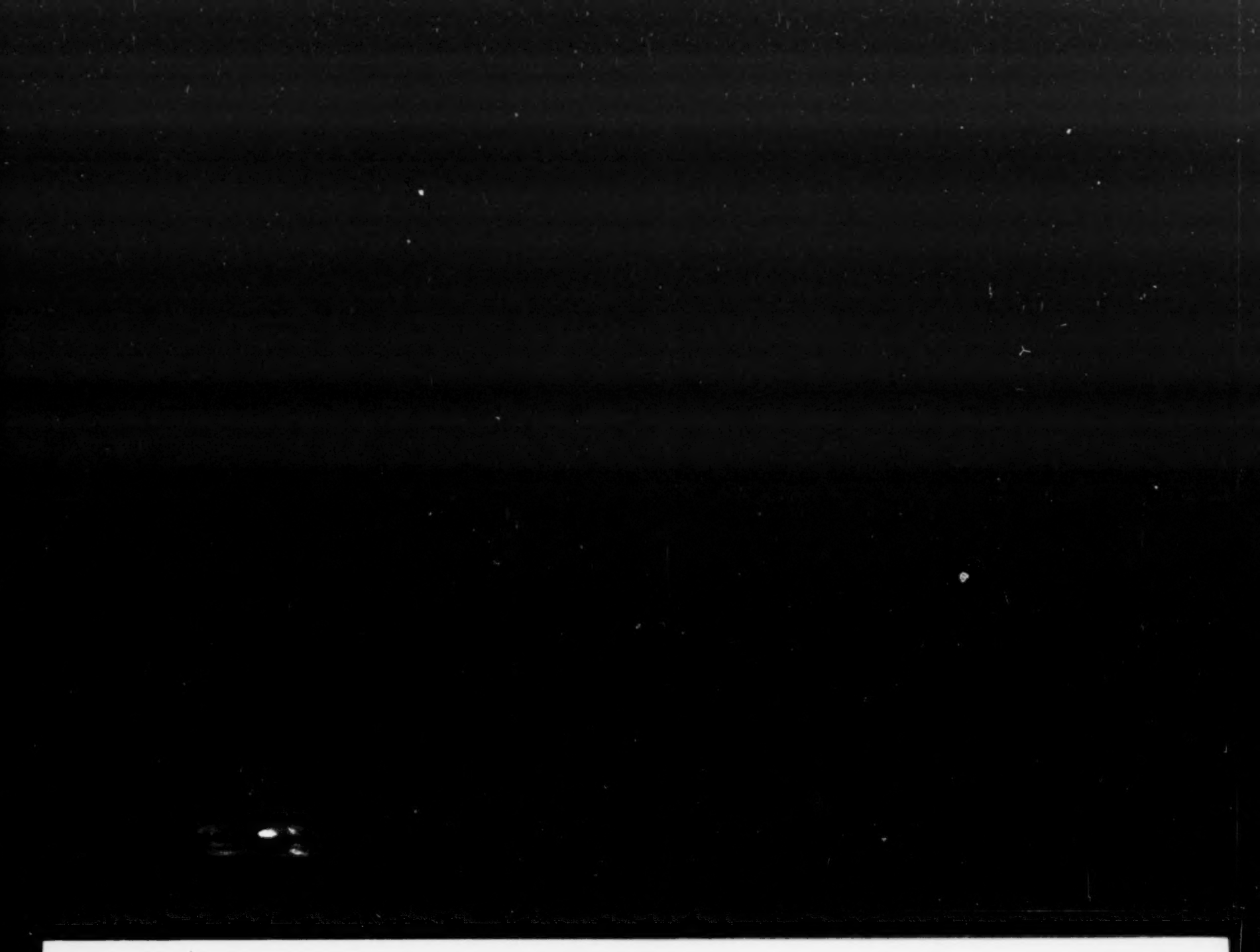
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